THE ECOLOGY AND BEHAVIOUR

OF

THE BLUE MONKEY

Cercopithecus mitis stuhlmanni

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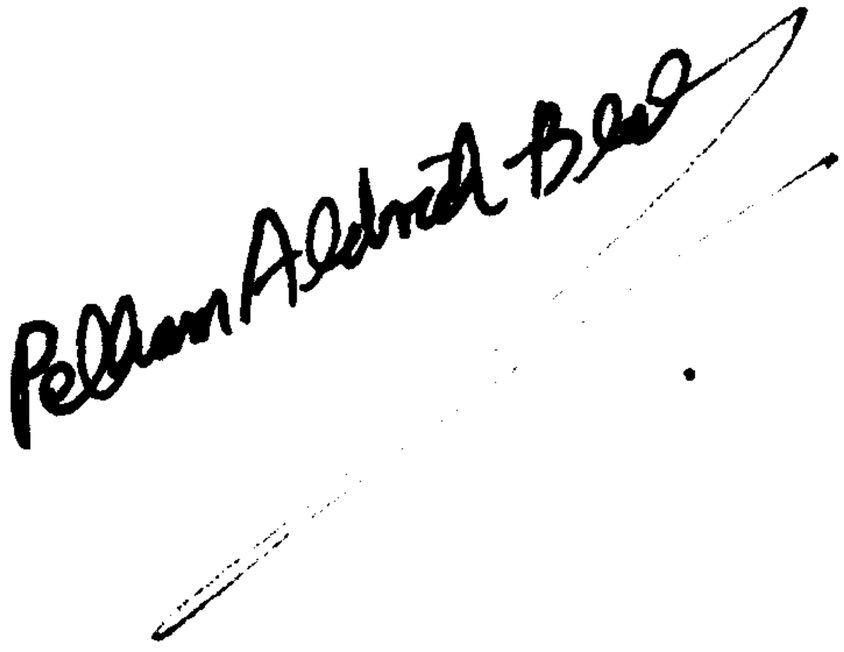
AS ORIGINAL

I declare that the design and execution of the studies on which this dissertation is based are my sole and unaided work unless otherwise indicated and acknowledged in the text, and that no part has been submitted for any other degree at any university.



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Chapter I

THE MONKEYS AND THE FOREST

INTRODUCTION

Serious primate field work, as distinct from the incidental and often anecdotal observations of early travellers, began with Carpenter's pioneering investigations of howler monkeys, red spider monkeys, and gibbons in the forests of Central America and the Far East (Carpenter 1934, 1935, 1940). The subject did not develop further until the early 1950's, with the establishment of long term studies on the Japanese macaque (e.g. Itani 1954, and many subsequent papers) and the work of Washburn, Hall and DeVore on savanna baboons in Africa (summarised in Hall and DeVore 1965, DeVore and Hall 1965). The last decade has seen a great expansion of interest in primate field studies, but research has not been spread evenly throughout the order. Most of the attention has been focused on savanna and open country animals rather than on the more numerous forest species. Some taxa such as the baboon-macaque group and the apes have been investigated fairly thoroughly, while others have been largely neglected.

The reasons for the initial concentration of research on terrestrial species are clear. Open

country animals are far easier to study than those living in dense vegetation. Once their confidence has been gained they can be followed throughout the day and long periods of concentrated observation are possible. Favourable conditions of observation permit the recognition of individual animals and hence detailed investigation of the relations between members of a troop. In contrast forest primates are difficult even to see, and even more difficult to follow. The return on time, energy, and money expended is correspondingly lower.

In addition, much of the earlier work on primates in the 1950's was carried out by people whose prime interest was in the making of inferences to the social evolution of man. It was thought that animals living in a habitat supposedly comparable to that of early man would provide the greatest insight into the problems faced by our simian forbears. Under the circumstances, concentration of research on open country primates was a perfectly reasonable strategy.

It has, however, had certain unfortunate consequences. In the early stages of the development of primatology the great diversity of social organisation to be found within the order was not suspected. For instance in 1961 Washburn and DeVore

wrote of baboons: 'Although monkeys and apes certainly differ in their behaviour from one species to the next, we believe that the main points ... would not be greatly changed by substituting other nonhuman primate species for baboons'. (Washburn and DeVore 1961). It is doubtful whether they would be so sanguine on the subject today. As the scope of field studies increased, it became apparent that there was considerable variation in social structure not only between but within species, and attempts were made to relate such contrasts to differences in habitat (e.g.: DeVore 1963, Crook and Gartlan 1966). Early hypotheses as to the determinants of social organisation suffered from two great drawbacks. Firstly, there was little detailed information on forest monkeys to go on, and authors were forced to rely to a large extent on fragmentary and incidental accounts. It will be shown that such initial impressions and short term studies can be highly misleading. Secondly, most of the reliable accounts of forest monkeys were of New World species; comparisons between savanna and forest monkeys therefore contrasted South American monkeys and to a lesser extent Old World colobinae with Old World cercopithecinae. It was not clear whether contrasts

in social organisation were dependent wholly on differences in habitat, or in part to differences in genetic constitution and basic behavioural repertoire. A more reliable picture would be obtained by comparing African forest cercopithecines with open country cercopithecines on the one hand and forest colobines and New World monkeys on the other, but the necessary information is only now becoming available.

At the time that this project was being planned (1964) there was no detailed account of the social organisation of any forest cercopithecine. Chalmers' valuable study of the black mangabey, Cercocebus albigena, (Chalmers 1967, 1968a,b,c) had yet to be completed. Haddow's paper on the redtail monkey, Cercopithecus ascanius, (Haddow 1952) contains little concrete information on social organisation, nor is it intended to be an authoritative statement on this aspect of the animal's biology. Likewise the many papers by Haddow's colleagues at the Virus Research Institute at Entebbe (e.g.: Haddow, Smithburn, Mahaffy, and Bugher 1947, Lumsden 1951, Buxton 1952) consider aspects of primate behaviour only inasmuch as they are relevant to epidemiology. Within the genus Cercopithecus the only studies other than Haddow's and his colleagues' were those of Gartlan

(1966) and Struhsaker (1967a,b,c,d) then in progress on C.aethiops, the vervet monkey. The vervet is not a forest species, but is found rather in woodland savanna and strips of riverine vegetation. It is therefore the least typical member of the genus in its choice of habitat. Hence a study of a forest Cercopithecus such as the blue monkey should help to fill a significant gap in our knowledge and provide useful material for comparison with other species.

Since 1964 the literature on forest monkeys has expanded considerably. In West Africa research has been carried out on Miopithecus talapoin (Gautier-Hion 1966, 1968, 1970) and on a variety of Cercopithecus spp (Gautier and Gautier-Hion 1969, Gautier 1969, Bouliere, Bertrand and Hunkeler 1969, Struhsaker 1969, Gartlan and Struhsaker in press). The limited information on African colobines (Booth 1957 on Procolobus verus, Ullrich 1961 on Colobus guereza) has been supplemented by the more detailed studies of Schenkel and Schenkel-Hulliger (1967) and Marler (1969a) on the latter species. As regards Asian colobines Jay's (1965) work on Presbytis entellus has been complemented by that of Sugiyama (1964, 1965a,b,c, 1966, 1967) on the same species, and Bernstein (1968) on Presbytis cristatus. Forest

populations of rhesus, Macaca mulatta, (Neville 1968) and lion-tail macaques, Macaca silenus, (Sugiyama 1968a) have received some attention, though less than macaque populations living under more open conditions. In the New World the howlers, Allouatta palliata, of Barro Colorado, the object of studies by Carpenter (1934), Colias and Southwick (1952), Altmann (1959), and Bernstein (1964), continue to be investigated (e.g.: Chivers 1969), and there have been field studies of other species such as Callicebus moloch (Mason 1966, 1968). Unfortunately this increase in quantity has not always been accompanied by an increase in the quality and reliability of the observations and the conclusions drawn from them.

TAXONOMY AND DISTRIBUTION OF THE C.MITIS GROUP.

The blue monkey belongs to a large assemblage of guenons generally known as the Cercopithecus mitis group and embracing the blue and Sykes' monkeys of East Africa and the samangos of southern Africa. Along with the rest of the genus Cercopithecus this group has suffered many vicissitudes at the hands of succeeding reviewers. Early reviews suffered from all the worst defects of museum taxonomy: the precise geographical origin of most specimens was of necessity obscure ... the type specimen of Sykes' monkey was purchased in Bombay and assumed to have come from Madagascar! ... and the range of variation within species was imperfectly known. This greatly hampered the r ecognition of valid taxa. The position was further complicated by the several different levels of relationship within the genus. If generic status is retained for the Cercopithecus grouping as a whole, and its relationship with other Catarrhine groups necessitates this, then the lower taxonomic divisions of species and sub-species are inadequate to deal with the varied degrees of affinity within the genus and additional taxa such as sub-genus or superspecies have to be employed.

The first scheme of classification to bear much resemblance to any in use today was that of Pocock (1907). He divided the genus Cercopithecus into 13 groups. Of these, two, the Albogularis and Leucampyx groups, were equivalent to the modern single C.mitis group. Elliot (1913), in his 'Review of the Primates', followed the same general scheme, but resuscitated the old generic name Lasiopyga. Members of the modern C.mitis group were divided between two sub-genera, Melanocebus and Insignicebus. Schwarz (1928) combined these two groupings to give a unified C.mitis group, a scheme that until recently has been followed by all subsequent reviews. The number of sub-species recognised varies slightly, but is usually about 20.

As Booth (1962) points out, the main defect of this scheme is that it conceals an apparently genuine sub-division within the group. The races of C.mitis to the east of the Kenya rift valley ('Sykes' monkeys) are distinct from those to the west ('blue' monkeys). 'Sykes' monkeys have a white throat patch, a head generally paler in colour than the back, and always some red on the lower back, whereas typical 'blue' monkeys have a dark head and no white throat patch. Both apparently show a north-south clime, to the east and west of the rift respectively.

The most recent review, Osman Hill (1966), recognises this sub-division. Osman Hill divides the genus Cercopithecus into nine superspecies, of which C.mitis is one. The C.mitis superspecies is further divided into three species, each with several sub-species (see Fig. 1.1). Two, C.mitis and C.albogularis, correspond to the Albogularis and Leucampyx groups of Pocock, and the third is formed by the inclusion of C.nictitans, an allopatric West African species. Osman Hill states that the rift valley forms a barrier to intermingling of the mitis and albogularis groups, ' ... hence their divergence, but whether this divergence is sufficient to warrant more than sub-specific status is a moot point'. C.mitis stuhlmanni and C.albogularis kolbi interbreed readily in captivity (C.P. Booth, pers comm), and some races such as C.mitis opisthostictus appear to be intermediate between the two groups. On the other hand there is no evidence for intergrading between C.mitis opisthostictus and C.albogularis moloneyi in Zambia where their ranges are separated by only a few miles (Osman Hill 1966), whereas in other parts of the same country intermediates between C.albogularis moloneyi and C.albogularis erythrarchus have been recorded (Ansell 1960).

Fig. 1.1 Classification of the C.mitis group, after Osman Hill (1966).

Superspecies C.mitis Wolf 1822

1. C.mitis Wolf 1822

C.m.mitis Wolf 1822
C.m.boutourlinni Giglioli 1887
C.m.stuhlmanni Matschie 1893
C.m.doggetti Pocock 1907
C.m.maesi Lonnberg 1919
C.m.kandti Matschie 1905
C.m.schoutedeni Schwarz 1928
C.m.opisthostictus Sclater 1893

2. C.albogularis Sykes 1831

C.a.albotorquatus Pousargues 1896
C.a.albogularis Sykes 1831
C.a.monoides Geoffroy 1841
C.a.phylax Schwarz 1927
C.a.kibonotensis Lonnberg 1910
C.a.kolbi Neumann 1902
C.a.moloneyi Sclater 1893
C.a.francescae Thomas 1902
C.a.nyasae Schwarz 1928
C.a.erythrarchus Peters 1852
C.a.schwarzi Roberts 1931
C.a.samango Wahlberg 1844

3. C.nictitans Linnaeus 1766

C.n.nictitans Linnaeus 1766
C.n.martini Waterhouse 1841
C.n.stampflii Jentink 1888

A possible criticism of Osman Hill's classification is that it implies an equal degree of relationship between C.mitis, C.albogularis, and C.nictitans. While the two former species are clearly closely related their connection with C.nictitans appears more tenuous. Unlike its immediate predecessors, though, the scheme has the advantage of recognising some sub-division of the C.mitis group. The separation of C.mitis and C.albogularis will therefore be followed in this dissertation. The term 'the C.mitis group' will be used to refer to the two species combined.

The distribution of the C.mitis group has been outlined by Tappen (1960), and detailed records for the individual sub-species are summarised by Osman Hill (1966). Isolated populations are found, wherever suitable habitats occur, from Ethiopia south through East Africa, Zambia, Rhodesia, Malawi and Mosambique to Natal, and west through the eastern part of the Congo to Angola. High forest is the typical habitat, though in some parts of the range the monkeys extend out into riverine forest or woodland savanna. Fig. 1.2 summarises available information on the distribution of the group.

CONTAINS

PULLOUTS

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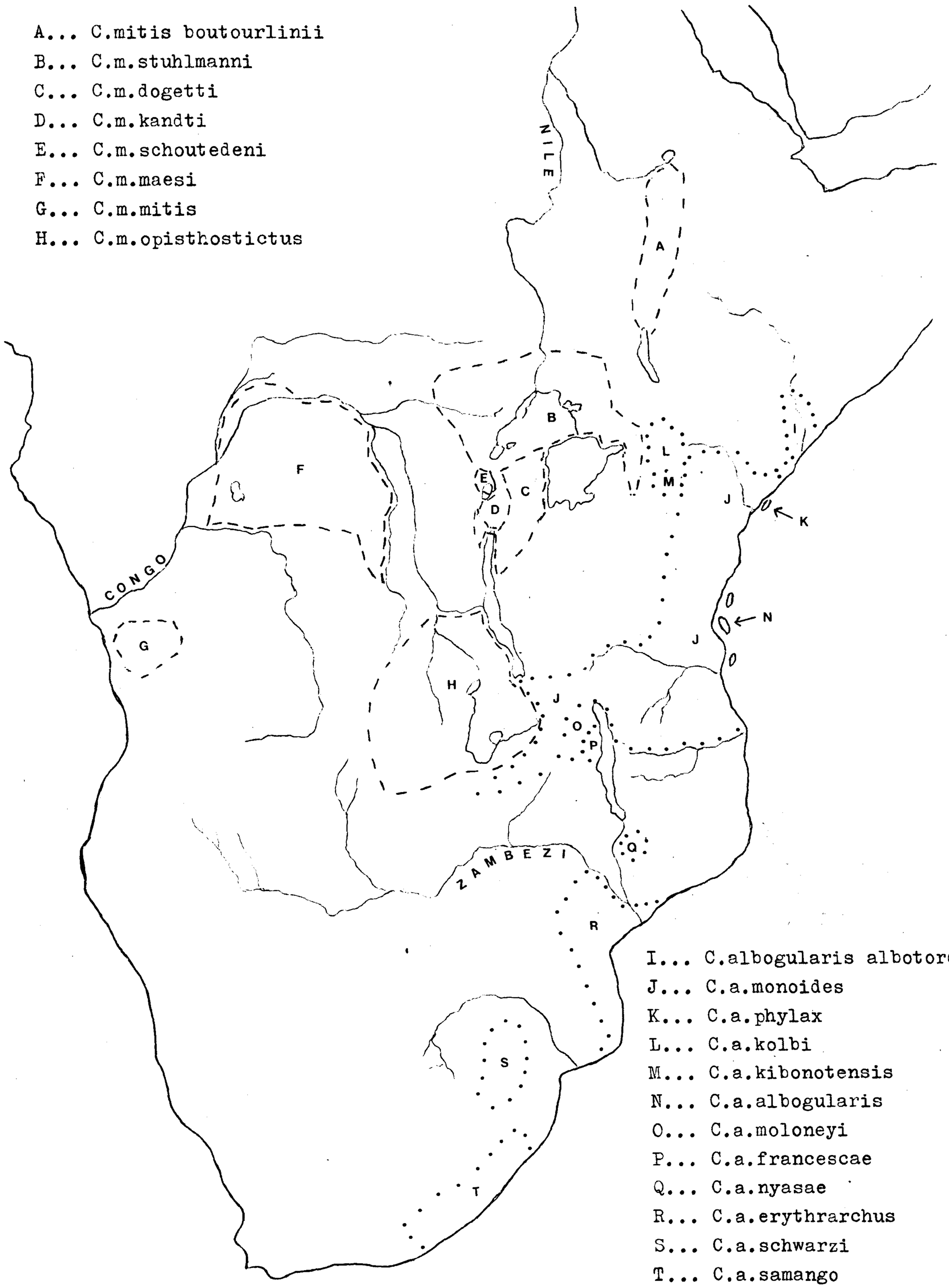
FIG.1.2 DISTRIBUTION OF THE C.MITIS GROUP.

(After Osman Hill 1966)

A... C.mitis boutourlinii
B... C.m.stuhlmanni
C... C.m.dogetti
D... C.m.kandti
E... C.m.schoutedeni
F... C.m.maesi
G... C.m.mitis
H... C.m.opisthostictus



I... C.albogularis albotorquatu
J... C.a.monoides
K... C.a.phylax
L... C.a.kolbi
M... C.a.kibonotensis
N... C.a.albogularis
O... C.a.moloneyi
P... C.a.francescae
Q... C.a.nyasae
R... C.a.erythrarchus
S... C.a.schwarzi
T... C.a.samango

(Ranges are discontinuous within the limits shown)

The pattern of distribution is totally different to that of any other Cercopithecus species. The only other member of the genus that extends so far to the south and east of the continent is C.aethiops, but this is not a forest monkey. Most of the remaining Cercopithecus spp are centred on the great forests of the Congo and West Africa. No other forest Cercopithecus is found east of the Kenya rift valley, and only C.ascanius and C.neglectus reach further east than Uganda. This pattern of distribution raises two questions; firstly, how did the C.mitis group come to occupy such a discontinuous distribution, and secondly, why do no other Cercopithecus species show a comparable pattern?

Some insight into these problems can be gained from a consideration of the past geological, climatic, and vegetational history of Africa. Moreau (1966) gives an outline of recent changes, particularly during the late Pleistocene.

Most of the major topographical features of the continent are of comparatively recent origin. The highland areas and great volcanoes of the eastern part of Africa owe their existence to a period of orogenic activity during the Pliocene, and the deepening of the rift valleys, the filling of the Lake

Victoria basin and the draining of the huge lake that occupied the Congo basin took place only during the Pleistocene.

The Pleistocene climate of Africa has been the subject of considerable discussion. At one time it was thought that the glaciations in Northern Europe corresponded precisely to periods of heavy rainfall over the whole of Africa (the pluvial theory, Nillson 1932), but this idea is no longer accepted (see, for example, Bakker 1966). There is ample evidence for great climatic changes during the Pleistocene, but these were not synchronised over the continent as a whole and periods of high rainfall did not necessarily correspond to glacial advances in higher latitudes. This is not to say that the glaciations were without influence on the climate in the tropics; temperatures would undoubtedly have been lower, and one possible effect of the lowering in temperature would be an increase in rainfall.

When one attempts to reconstruct past vegetational changes, disagreement becomes more acute. Today forest is largely confined to the Congo basin, a strip extending up to 200 miles inland from the northern coast of the Gulf of Guinea, and isolated highland areas mainly in the south and east of the continent.

The montane forests are separated by tracts of more open country inimical to forest animals. To account for the present distribution of the mitis group one must postulate either that these isolated forests were once continuous or alternatively that the monkeys were formerly less exclusively arboreal.

At present there is a well defined boundary between 'montane' and 'lowland' vegetation at an altitude of about 5000 ft. Analysis of pollen samples from the major mountain ranges of East Africa suggests that at the height of the last glaciation, between 25,000 and 15,000 years ago, the boundary was about 3300 ft. lower. If the present lapse rate of temperature with altitude then pertained temperatures must have been around 5°C lower than they are today. Hence unbroken montane conditions would have extended from Ethiopia through East Africa south to the Cape Province and west to Angola, an area which corresponds precisely to the present range of the C.mitis group.

But here one must sound a note of caution. To conclude that unbroken forest extended over the whole area would be unjustified. The effects of a drop in temperature on rainfall and humidity would vary with local topography. The presence of forest is affected not only by total rainfall but also by the

distribution of precipitation over the year. For instance, in southern Uganda an annual rainfall of 45" supports forest whereas in the north of the country where there is a severe dry season 60" is barely adequate (Langdale-Brown, Osmaston and Wilson 1964). It has even been argued that, strictly speaking, the palynological data fails to provide conclusive evidence for any extension of montane forest. For instance Kendall (1969) points out that the Kenyan sample sites are in the present upper reaches of the forest, and show a replacement of forest pollen by grains characteristic of the ericaceous and alpine zones above. All that can be concluded, he argues, is that these zones extended lower than they do now. He suggests that Moreau is unjustified in postulating a corresponding downward extension of the forest belt; it might rather have contracted or even disappeared.

On balance, though, the consensus of opinion seems to be that during the cooler periods montane forests would have been much greater in extent than they are today, and many of the now isolated blocks would have been continuous. Conversely during inter-glacials the lower limit of montane vegetation would have been raised, though only by about 1300 ft. and

the area of forest correspondingly reduced. Moreover the modern limits of forest may in certain cases represent an absolute minimum; there is evidence that many forests have been reduced by human activity in the comparatively recent past. Even if adjoining blocks of forest failed to become continuous, the intervening country may have presented a lesser barrier to movement of monkeys than a gap of similar size would today. The relatively open savanna that covers much of eastern and southern Africa may be a fire climax induced by man; the primeval vegetation probably included a higher proportion and greater variety of trees and bushes. Hence the present discontinuous distribution of the C.mitis group can readily be accounted for by changes in the pattern of vegetation.

To explain the absence of other forest Cercopithecus spp from the greater part of the mitis group's range Tappen (1960) suggests that its major extension must have taken place during an early spread of montane forest, prior to the main Cercopithecus radiation. The mitis group would thus represent an ancestral Cercopithecus stock, whereas other members of the genus would be of more recent origin.

The diploid chromosome number of C.mitis is 72;

other Cercopithecus spp, apart from C.l'hoesti, have between 58 and 70 chromosomes, with some variation between individuals of the same species (Boroankar 1966, Chiarelli 1968). Opinions differ as to the significance of such counts. Hammerton (1963) and Bender and Chu (1963) suggest that numbers have evolved from higher to lower by centric fusion mechanisms comparable to those demonstrated for other mammals. Chiarelli (1968), on the other hand, regards this hypothesis with disfavour, and suggests that the reverse may be the case.

If the antiquity of the C.mitis group is accepted, the relative lack of divergence within the group as against the great evolutionary radiation shown by the rest of the genus has somehow to be explained. Tappen suggests that this lack may be due to a comparative absence of competition from other monkeys, but such an argument is surely circular. An alternative explanation may be sought in the history of the Congo and Upper Guinea forests. These forests are too low lying to be affected by downward shifts of the montane boundary, but are vulnerable to changes in overall precipitation. Much of the present Congo forest is rooted in Kalahari sand dating from an arid period at the end of the

middle Pleistocene, and there were further dry periods around 40,000 and 10,000 years ago. It is not clear whether these arid spells were general over central and western Africa or whether they merely represented a northwards shift of the equatorial rain belt, and hence the forest also. However it seems certain that the present Congo forest was fragmented to an enormous extent at some time prior to 50,000 years ago. Likewise the Upper Guinea forest would have been equally fragmented about 22,000 years ago, when the Sahara extended 300 miles to the south of its present limits. Hence these forests are of more recent origin than the montane forests, and have suffered greater vicissitudes during the last few thousand years.

These unstable conditions would result in frequent isolation of monkey populations, giving opportunities for differentiation at both specific and subspecific levels. The larger rivers would act as further barriers. For instance Booth (1958), in his discussion of the zoogeography of West African primates, suggests that their present distribution can best be interpreted by postulating the fragmentation of the Upper Guinea forest into isolated refuges during dry periods, and the effectiveness of the Niger as a

barrier to movement. (See also Moreau 1969 for a reassessment of the zoogeography of primates and other forest vertebrates in this region). Likewise Tappen (1960) points out that within the Congo forest the ranges of many species are bounded by the Congo and Lualaba rivers.

In contrast, the various races of the C.mitis group may never have been separated for sufficiently long at a stretch for genetic and behavioural isolation to develop, and so at each extension of the forest they would intermingle and produce hybrid swarms. Though the montane forests would have been subject to some fluctuations they would at least remain in much the same place, being based as they are on static topographical features. The Congo and Upper Guinea forests would show no such regular waxing and waning; rather the basic pattern of distribution would change.

If this argument is correct it follows that many of the modern races of the C.mitis group are of recent origin, having been isolated only since the end of the last glaciation. In some cases the time of isolation can be fixed quite accurately. For instance the island of Zanzibar was cut off from the mainland only 10,000 years ago, by the rise in sea level resulting from the melting of the icecaps in

higher latitudes (Moreau 1966). Monkeys from the island are consistently smaller and paler in colour than those on the adjacent mainland, and are classified as a separate sub-species, C.a.albogularis rather than C.a.monoides. On the other hand the nearby island of Mafia has been isolated for a shorter period, and no such divergence has arisen.

Isolation does not in itself necessarily result in differentiation, nor are rates of divergence the same in different populations. The size of the population and the ecological pressures operating on it also play a part. However in general one might expect a broad correspondence between length of isolation and degree of differentiation. This being so, the evolution of the various differences in pelage within the group presents some puzzling features. If the division into mitis and albogularis subgroups represents a genuine evolutionary dichotomy, then the most effective barrier to interbreeding at times of forest recession should be a north-south line following the rift valley. Yet examination of a contour map of Africa shows that the first breaks to develop in the continuity of montane conditions would be east-west lines in the vicinity of Lake Rudolf and the Zambesi and Limpompo rivers. Indeed

in the L.Naivasha-L.Nakuru area the floor of the rift is over 6000 ft. above sea level and should hardly provide a barrier at all, yet the populations on the two sides of the valley are classic representatives of the two species within the group. This of course assumes a precise correspondence between altitude and the extent of forest conditions, and ignores the possible effects of local climatic variations and human influence on the spread of forest. Nevertheless it seems possible that the north-south clines within the C.albogularis and C.mitis subgroups may be just as important from an evolutionary point of view as the east-west dichotomy within the group as a whole. Insofar as a scheme of classification should represent an evolutionary relationship rather than just a convenient 'filing system', the classification of the group may require further revision. For the present, however, this must await a more complete elucidation of its past history.

THE BLUE MONKEY

Distribution.

The blue monkey, C.mitis stuhlmanni, is found in forests in the eastern Congo, Uganda, the southern Sudan, and western Kenya (see fig. 1.3). Records for the Congo are summarised in Osman Hill (1966). In Uganda, Haddow (1956) records it in the Budongo, Bugoma, Semliki, Kibale, Ruwenzori, and Kalinzu forests in the west of the country, and on Mt. Elgon in the east. It is also found in the Impenetrable forest (Stott 1960, and pers.obs.), the Maramagambo forest (Laws, pers.comm.), the Mafuga forest (pers. obs.), and montane forests on Kadam, the Nangeya Mts, and the southern slopes of the Imatongs (Uganda Game Dept. maps). In the Sudan it is common in forests on the Imatong, Didinga, and Dongotona Mts. (Butler 1966). In Kenya, it is present in the Kakamega forest and in forests on the Mau plateau, to the west of the rift (Schwarz 1954). Schwarz gives the southernmost locality as Mbulu, 60 miles south of Ngorongoro in the crater highlands of Tanzania, but skins in the British Museum collection from the Manyara forest, on the floor of the rift but between these two localities, fall within the range of

variation of C.mitis kibonotensis from Kilimanjaro and Meru. It is hence possible that the Mbulu record may refer to this race, the Kilimanjaro blue monkey.

These localities include a wide range of forest types, from moist evergreen forest and moist semi-deciduous forest to moist montane forest, alpine bamboo, and in the north of the range dry montane forest (see fig. 1.4). The upper limit of the range in Ruwenzori is at around 10,000 ft, at the top of the bamboo zone; it appears not to extend into the ericaceous zone above. Much of the Mafuga forest has been cleared and planted with softwoods, mainly Pinus patula and P.radiata. Blue monkeys are not uncommon in the plantations, but seldom damage the trees by gnawing the bark or eating the leading shoots as does C.a.kolbi in plantations in the Kenya highlands.

A surprising feature of the blue monkey's distribution in Uganda is its absence from the Mabira and South Mengo forests in the centre of the country. These forests differ but little in floristic composition from others in which blue monkeys do occur, yet they are inhabited only by redtails, Cercopithecus ascanius, and black mangabeys, Cercocebus

FIG. I.3 DISTRIBUTION OF THE BLUE MONKEY

Underlined names denote forests in which blue monkeys are found

....Forest

.....International boundary

SUDAN

DIDINGA MTS.

IMATONG MTS.

NANGEYA MTS.

DONGOTONA MTS.

L. RUDOLF

UGANDA

MOROTO

ITURI

BUDONGO

L. ALBERT

KADAM

KENYA

BUGOMA

ELGON

CONGO

ITWARA

SEMLIKI

KIBALE

MABIRA

SOUTH MENGO

KAKAMEGA

RUWENZORI

KALINZU

MARAMAGAMBO

MAU PLATEAU

ABERDARES

L. VICTORIA

IMPENETRABLE

MAFUGA

Fig.1.4. Forest types of blue monkey habitats in Uganda.

FOREST	TYPE (from Langdale-Brown et al, 1964)
Budongo	Moist semi-deciduous (Celtis - Cynometra)
Bugoma	Moist semi-deciduous (Celtis - Cynometra)
Kibale	Moist evergreen (Parinari) / Moist semi-deciduous (Celtis - Cynometra)
Semliki	Moist semi-deciduous (Celtis - Cynometra)
Ruwenzori	Moist montane (Pygeum / Hagenia - Rapaena) / Bamboo
Kalinzu	Moist evergreen (Parinari)
Maramagambo	Moist semi-deciduous (Celtis - Cynometra)
Impenetrable	Moist evergreen (Parinari)/moist montane (Pygeum)/Bamboo
Mafuga	Moist montane (Pygeum), and softwood plantations.
Elgon	Moist montane (Pygeum/Hagenia - Rapaena)/Bamboo
Kadam	Dry montane (Juniperus - Podocarpus)
Nangeya Mts.	Dry montane (Juniperus - Podocarpus)
Imatong Mts.	Dry montane (Juniperus - Podocarpus)

albigena. (The black and white colobus in the small patch of forest in the Entebbe botanic gardens were introduced artificially). It is conceivable that blue monkeys may at one time have been found in these forests and were exterminated by hunting, but there does not appear to be any tradition for the use of their skins among the Baganda.

An alternative explanation is that the forests may be of relatively recent origin and blue monkeys may never have had the opportunity to colonise them. Analysis of sediment cores covering the past 15,000 years from the northern shores of L.Victoria shows that, within this period, forest first appeared in the area about 12,000 years ago (Kendall 1969). The inference that rainfall must have increased at that time is in accord with climatic changes already established for montane and rift valley locations elsewhere in East Africa. However this does not necessarily mean that the northern shores of the lake would have been forested during other, earlier pluvials. At present the forests owe their existence primarily to the heavy rainfall received from the lake. Prevailing winds are from the south east. On the S.E. shore of the lake rainfall is only 15" per annum, but by the time the winds reach the N.W. shore they have been recharged with moisture and

rainfall there is in general 45" - 55". Were the lake smaller in extent, or different in shape, the south east monsoon would be recharged to a lesser degree. Since the Victoria basin filled only during the Pleistocene, the lake may only recently have attained a size sufficient to give enough rain to support forest.

The blue monkey's range abutts on that of three other races of the C.mitis group, the Sykes' monkey, C.m.kolbi, the golden monkey, C.m.kandti, and the silver-backed monkey, C.m.doggetti. Blue and Sykes' monkeys are separated in Kenya by the rift valley. The boundary between the blue monkey and other two races is less well defined, but both golden and silver-backed monkeys appear to be more restricted in their choice of habitat than the blue monkey. In Uganda silver-backed monkeys are found in swamp forests around Sango Bay on the western shore of Lake Victoria (Malambigambo, Tero, Kaiso, and Namalalu forests), and along the Kagera river, and in swampy valleys in the Impenetrable forest (Haddow 1956). They are said to feed on the submerged bases of papyrus stems. The golden monkey is a montane species, being found typically in bamboo forest. It is centred on the mountains around Lake Kivu; in Uganda it is found on

the Virunga volcanoes and in the Echuya bamboo forest in Kigesi (Haddow 1956, and pers.obs.), and it is said to occur also in the Impenetrable forest (J.G. Williams, pers.comm.). If this is so, all three races occur in the same forest, though presumably in different ecological niches. A short visit to the Impenetrable forest failed to confirm the presence of any race other than the blue monkey, and blue monkeys were abundant in the bamboo zone where one would expect golden monkeys to be were they present. Further investigation of the situation would be desirable, but unluckily this forest is particularly difficult to work in.

Description.

Blue monkeys are predominantly black and grey in colour. The top of the head is black, the face grey ('grey' in this context denoting an intermediate shade of grey), and the cheek fur pale grey. There is a conspicuous pale grey band across the brow. The eyes are brown. The back, hindlegs, and most or all of the tail are grey. The forelegs, hands, and feet are black, and the distal few inches of the tail may be black or dark grey. The underside is pale grey. (See frontispiece and fig. 1.5) The ischial callosities are grey, and the hair around the anal region may have

FIG. I.5 Blue monkey in flowering Khaya anthotheca.

a reddish-brown tinge. In the male, the scrotum and the penis are grey; hence the genitals, unlike those of other species such as the vervet, do not contrast with the surrounding fur. The nipples of females vary in colour from whitish-grey through pale pink to bright pink. There are no clear cut differences in pelage between males and females. The newborn infant's natal coat is not strikingly dissimilar in colour to that of the adult, but the contrasts between different parts of the body, and particularly the pale brow band, are less distinct and the fur is 'fuzzier' in texture. At birth the ears are pink, but they turn grey within a few days.

Little quantitative information on weights and dimensions is available. Osman Hill (1966) summarises what little is known. Mature males probably weigh 15-17 pounds, and females 9-12 pounds. There is thus a substantial discrepancy in size between the sexes.

There is considerable variation in colouration, both in the sub-species as a whole and within individual populations. The extent of black on the extremities varies widely. The tail may be grey throughout or have a distinct black tip, or it may be dark grey at the distal end. The black on the

hindlimbs may be confined to the feet or spread up onto the legs also. Likewise the black on the forelimbs and crown of the head may extend onto the nape of the neck to join up and form a continuous black cape. The brow band, cheek fur, and back of blue monkeys in the Mafuga forest had a distinct yellow-brown tinge, and some monkeys from other forests also had a hint of brown on the lower back.

Although variations in appearance would no doubt be sufficient to permit recognition of individuals under ideal observational conditions, as for example in captive groups, this was seldom possible in the field. Lighting conditions in the canopy were such as to render the precise distinction of minor differences in shades of grey or black exceedingly difficult. For instance one cannot tell whether the final 3" of a monkey's tail are dark grey or black if all that can be seen is a silhouette 150 ft. up in the treetops. Such few individuals as were clearly recognisable usually had some peculiarity, such as a kink in the tail, a piece missing from one ear, or a growth on the rump. At first it was thought that nipple size and colour might provide a useful means of distinguishing between females, but although these were subject to considerable variation they did not remain constant over long periods. Their value was

therefore confined to helping to tell females apart during single periods of observation, or more rarely over a few days' sightings. Females with babies could sometimes be recognised from a combination of their own and the babies' appearance, but such females were more retiring in their habits which tended to cancel out the advantage of potentially easier recognition.

Classification of sex and age classes.

Six categories were recognised; mature male, young adult male, adult female, juvenile, infant and baby.

Mature males were substantially larger than a typical adult female; males take five years to mature as against three years for females (Kenya Forest Dept. memo, 1964). In the field they could be recognised on size alone. Under favourable conditions of observation the genitals could be seen also, but as they are not conspicuously coloured they are of little practical value as an aid to initial identification.

Young adult males were younger males similar in size to an adult female. This class presented the greatest problem of identification. Even under ideal conditions the genitals were seldom visible, being less developed than in a mature male. They had

generally to be sexed on the somewhat negative grounds of appearing to have no nipples. There are slight differences in build between such males and females; the males are less gracile and have larger feet, but these contrasts are only evident at close range and after much practice.

Adult females generally had conspicuous nipples. However in most monkeys the nipples become prominent only after the first baby has been born; the nipples of nulliparous females may be hidden by the fur. There is hence scope for confusion between nulliparous females and young adult males, as they are similar in size and neither have readily visible external genitalia or secondary sexual characters. At close range they could usually be distinguished by the differences in build noted above.

The juvenile and infant classes were made up of monkeys approximately two thirds and one third of adult size respectively. It was not possible to sex them in the field. Babies were classified as such for the first two and a half months of life, while they were still carried by their mothers. When they attained greater independence and started to move by themselves they were classed as infants.

In practice the monkeys could not always be seen

well enough to fit them into any category with certainty, except in the case of mature males. Many interactions were therefore incompletely documented, and further categories such as 'unsexed adult' and in extreme cases 'unclassified' have to be used in the analysis of data.

THE STUDY

Twenty months, from August 1965 to March 1967, were spent in Uganda. Of this period about five months were lost as a result of sickness, civil war, and sundry other distractions. Most of the field work was carried out in the Budongo forest. This forest was chosen because it is readily accessible, has a large population of blue monkeys, and is not too difficult to penetrate compared to some other Ugandan forests. Its ecology is fairly well known, and another member of the primate fauna, the chimpanzee, has already been studied (Reynolds and Reynolds 1965) Eggeling (1947) gives a general description of the ecology of Budongo, and further information can be found in the various Forest Department working plans of which that by Philip (1965) is the most recent.

Blue monkeys were observed for 450 hours in Budongo, mostly between December 1965 and March 1967.

They were also watched for short periods in the Bugoma, Kibale, Ruwenzori, Impenetrable, Mafuga, and Mt. Elgon forests. The golden monkey, C.m.kandti, and the Sykes' monkey, C.a.kolbi, were watched briefly in the bamboo forests of the Virunga volcanoes in S.W.Uganda and the Aberdare Mts. of Kenya respectively.

The field work was supplemented by observations on small captive groups of Sykes' monkeys in the Dept. of Psychology at Bristol University and the Dept. of Zoology at Makerere University College in Uganda. Unluckily blue monkeys could not be obtained for this purpose; hence any comparisons between wild and captive groups must be made with caution.

THE BUDONGO FOREST.

Situation and topography.

The Budongo forest lies on top of the escarpment to the east of L.Albert between 1 35' and 1 55'N and 31 18' and 31 42'E, at an altitude of 3000 - 3600 ft. Budongo and the contiguous Siba forest cover an area of 160 sq. miles, of which the solid triangular block of Budongo proper accounts for 136 sq. miles and Siba, an amalgamation of strips of riverine forest lying to the south of the Masindi-Butiaba road, for the remainder. The area covered by the forest is gently

undulating, with a slight slope N.N.W. towards the escarpment where the ground drops more than a thousand feet, to the lake flats. Most of the valleys within the forest run from S.E. to N.W., and contain small streams or slowly draining swamps. As they approach the western edge of the forest the watercourses join to form two larger rivers, the Sonso and Waisoke, which cut through the escarpment and flow ultimately into L.Albert. During the rains these rivers may attain a depth of 4 ft. but in the dry season the Sonso often dries up completely. In the grasslands surrounding Budongo isolated hills affording good views over the forest (see fig.1.6) rise some hundreds of feet above the general level of the country.

Climate.

Rainfall is of the two peak type characteristic of most of East Africa. The first wet period is from the end of March to the end of May, and the second from August to the end of November. There is a pronounced dry season from mid December until mid February. Annual rainfall for the area is typically between 50" and 60", but varies from as little as 40" to as much as 85". Rainfall records for the study period for Nyabyeya, on the forest edge, and for a station 4 miles inside the forest are given in fig. 1.7.

The 1966/67 dry season was unusually severe. Most of the rain falls as violent thunderstorms, often very local in extent, in the afternoon and evening.

Maximum daily temperatures are between 85° and 90°F in the dry season and 75° and 85°F during the rains. Relative humidity varies from 45 - 50% in the dry season to 75% at other times.

Vegetation

Langdale-Brown et al (1964) classify Budongo as moist semi-deciduous forest on the Yangambi scale. Eggeling (1947) recognises four main types of forest: colonising forest, mixed forest, ironwood forest, and swamp forest. The first three belong to a single sere with ironwood forest as the climax of the succession. Swamp forest is an edaphic climax, being limited to areas where the water table is near or above the surface the whole year.

Colonising forest is of two distinct forms. On the richer soils the grassland is first invaded by a prickly shrub, Acanthus arboreus. This creates conditions suitable for the establishment of Maesopsis eminii, a fast growing, light demanding species, and in such areas Maesopsis forest results. The eponymous species accounts for almost all the even, closed canopy in this type of forest (see figs. 1.6 & 1.8).

On the poorer soils the grassland is colonised by a mixture of woody herbs and herbaceous climbers, amongst which trees such as Albizia spp, Caloncoba schweinfurthii, Croton spp, Olea welwitschii, Phyllanthus spp, Sapium ellipticum and Spathodea campanulata become established. These give rise to the form known as woodland forest. Unlike Maesopsis forest woodland forest has a very broken and uneven canopy. Besides shrub and herb layers both forms of colonising forest have two distinct tree layers. The upper canopy seldom attains more than 100 ft. in height, and the lower, closed canopy about 70 ft. Though creepers and soft-stemmed climbers are common, lianas are absent.

As the light demanding species of colonising forest are supressed and give way to more shade tolerant species it is gradually replaced by mixed forest (see fig. 1.9). Mixed forest is characterised by its four tree layers, its great diversity of species, many of which have large buttresses or flutings on their trunks, and by the abundance of epiphytes and lianas. The highest, emergent layer is dominated by the mahoganies Khaya anthotheca and Entandophragma spp, commonly associated with Chrysophyllum perpulchrum, Alstonia boonei, and Mildbraediodendron excelsum.

Trees in this layer often attain a height of 180 ft. or more. The upper continuous canopy, 70-120 ft. in height, commonly contains Celtis mildbraedii, Chrysophyllum albidum, Funtumia spp, Erythrophleum guineense, Cynometra alexandri, Celtis zenkeri, and Trichilia prieuriana. The two lower layers, up to 35 ft. and from 35-70 ft. in height, contain more shade-tolerant species such as Trichilia rubescens, Lasiodiscus mildbraedii, Rinorea ardesiflora, Teclea nobilis, and Celtis wightii. Epiphytic, semi-parasitic and self-supporting figs are numerous in all layers.

Ironwood forest is dominated by Cynometra alexandri, which accounts for virtually the entire upper canopy. In addition to young Cynometra the lower layers contain species such as Lasiodiscus mildbraedii, Strychnos mitis, Alstonia boonei, and Celtis wightii. The final transition to ironwood forest probably takes several hundred years. Cynometra now covers about 30% of the whole forest. It is thought that this area may correspond to the total extent of the forest prior to a wet period from 1400 - 1600 A.D., when considerable expansion took place (Philip 1965).

Swamp forest (see fig. 1.10) is confined to the wetter valley bottoms. It is typically two-layered,

FIG.1.6 A view of the Budongo forest from Busingiro hill. The area of level, uniformly shaded canopy in the middle foreground is Maesopsis forest. The more uneven canopy of an area of mixed forest stands out beyond.

Fig. 1.7 Rainfall records

(a) Nyabyeya

Month	(1965) R'fall	No.of rainy days	(1966) R'fall	No.of rainy days	(1967) R'fall	No.of rainy days
Jan	0.27"	1	1.92"	4	0.09"	1
Feb	0.32"	3	3.03"	9	0.70"	3
March	5.60"	15	3.66"	16	1.06"	4
April	2.03"	16	8.23"	22	(up to 14th)	
May	6.02"	15	4.15"	11		
June	2.06"	9	2.42"	12		
July	2.16"	12	4.64"	11		
Aug	6.64"	17	4.70"	12		
Sept	7.60"	16	6.49"	19		
Oct	10.85"	24	10.22"	17		
Nov	8.57"	20	8.08"	11		
Dec	3.07"	11	0.19"	2		
Total:	55.19"	159	57.73"	146		

(b) 4 miles inside forest

Month	(1965) R'fall	No.of rainy days	(1966) R'fall	No.of rainy days	(1967) R'fall	No.of rainy days
Jan	0.22"	1	1.93"	4	0.49"	1
Feb	1.45"	4	1.43"	8	0.27"	3
March	5.99"	11	6.73"	15		
April	5.59"	11	13.43"	22		
May	4.16"	13	4.40"	10		
June	2.23"	4	2.13"	9		
July	2.60"	8	5.46"	15		
Aug	6.73"	16	5.98"	9		
Sept	4.18"	14	8.09"	17		
Oct	12.56"	23	9.73"	16		
Nov	7.47"	22	5.67"	10		
Dec	2.36"	8	0.35"	1		
Total:	55.54"	135	65.33"	136		

FIG. I.8 A view of the forest edge and surrounding grassland. The white-stemmed trees on the forest edge and that emerging above the general level of the canopy are Maesopsis eminni. A belt of Acanthus arboreus separates the forest from the grassland.

FIG. I.9 Mixed forest.

FIG. I.IO Swamp forest. The big trunk on the right is Cynometra alexandri, and the palm-fronded climber Calamus sp.

but the canopy is very broken and uneven. As a result the shrub and herb layers are exceedingly dense. It is characterised by species such as Mitragyna stipulosa, Pseudospondias microcarpa, and Phoenix reclinata. The spiny, climbing rattan cane, Calamus sp. is a painfully obtrusive feature of such forest.

The forest is everywhere surrounded by grassland containing scattered trees, mainly Terminalia velutina. In some areas the grass is relatively short, Setaria and Brachiaria spp being dominant early in the year and Hyparrhenia spp from about June onwards. In others there are dense stands of elephant grass, Pennisetum purpureum, attaining a height of 10-12 ft. Most of the grassland is burnt annually in December or January. Except to the S.E. of the forest it is virtually uninhabited.

Exploitation and management.

Budongo contains many valuable timber trees, the most notable being the various mahoganies. Timber cutting began on a small scale in about 1910, but was sporadic until the early thirties. During this period there was also some tapping of wild rubber (Funtumia elastica). In 1935 the first working plan for the forest was prepared, and large scale but strictly controlled exploitation has continued since then. By

the end of 1964 over 15 million cubic feet of timber had been cut, two thirds of this being mahogany.

Initially no steps were taken to induce the regeneration of desirable timber species, but from the late thirties experimental work on the diffuse planting of mahogany striplings to supplement natural regeneration began. After some years it became apparent that only limited success was being achieved, and the scheme was discontinued. Various other treatments were tried, and it was finally decided that the spraying of unwanted trees with arboricides provided the best means of encouraging desirable species. Under the present scheme all but about thirty species are killed. This opens up the canopy and creates the same effect as a heavy felling. A dense tangle of shrubs and creepers results, providing ideal conditions for the natural regeneration of mahoganies and also ideal feeding conditions for elephants, which do great damage to the growing crop. It is hoped not only to increase the proportion of mahoganies and other valuable timber trees in mixed forest, but to arrest the natural succession to ironwood forest and reconvert existing ironwood forest to mixed forest. Though there is a market for Cynometra timber it is much less valuable

than mahogany. The long term effect on the overall ecology of the forest will obviously be profound.

Fauna.

The fauna of Budongo has many affinities with that of the Congo forest. Besides the blue monkey, four other diurnal primates are found in Budongo; the redtail monkey, Cercopithecus ascanius, the black and white colobus, Colobus guereza, the olive baboon, Papio anubis, and the chimpanzee, Pan troglodytes. All are common; sometimes all five species would be seen in a single day. Vervet monkeys, Cercopithecus aethiops, were occasionally seen in the savanna surrounding the forest, but never nearer than 200 yards to the forest edge.

The larger ground-dwelling mammals include elephant, buffalo, bushbuck, blue duiker, red forest duiker, bushpig, and giant forest hog. Leopards are not uncommon, though seldom seen, and there are reputed to be golden cat. Civet cats and genets were often seen on roads in the forest at night.

The avian fauna is rich and varied, and invertebrates of all forms abound.

STUDY AREA.

When I first arrived in Budongo I ranged widely

over much of the forest, but after surveying various possible study areas I confined my activities largely to a small area of about a quarter of a sq. mile on the S.W. edge of the forest (see fig. 1.11). A long strip 200-300 yards wide is here separated from the main part of the forest by a road which leads to the sawmill. The road is used by only a few cars a day, and by small numbers of Africans on foot. This traffic did not appear to disturb the monkeys; they would remain feeding near the roadside while cars and people passed provided they did not stop near them, and indeed monkeys in this area seemed less wild than ones deeper into the forest where people seldom penetrated. Any disadvantages from disturbance by passers by were more than cancelled out by the great benefit of having a rapid and easy means of access running through the middle of the study area. The road did not restrict the movements of monkeys, as along much of its length they could cross it without descending to the ground, but any movements across it were easily seen (see figs. 1.12 & 1.13). As movement on the outer side of the road was limited by the forest edge, monkeys in this narrow strip could be followed more easily than ones deep inside the forest where there were no obvious curbs on their movement.

The western part of the area is flat; the eastern part slopes gently down to the river Kamirambwa, the floor of the valley being perhaps 100 ft. below the general level of the surrounding country. The river varies in depth from a few inches to about three feet, and its bed is seldom wider than ten feet. Much of the valley bottom is swampy, and floods after heavy rain.

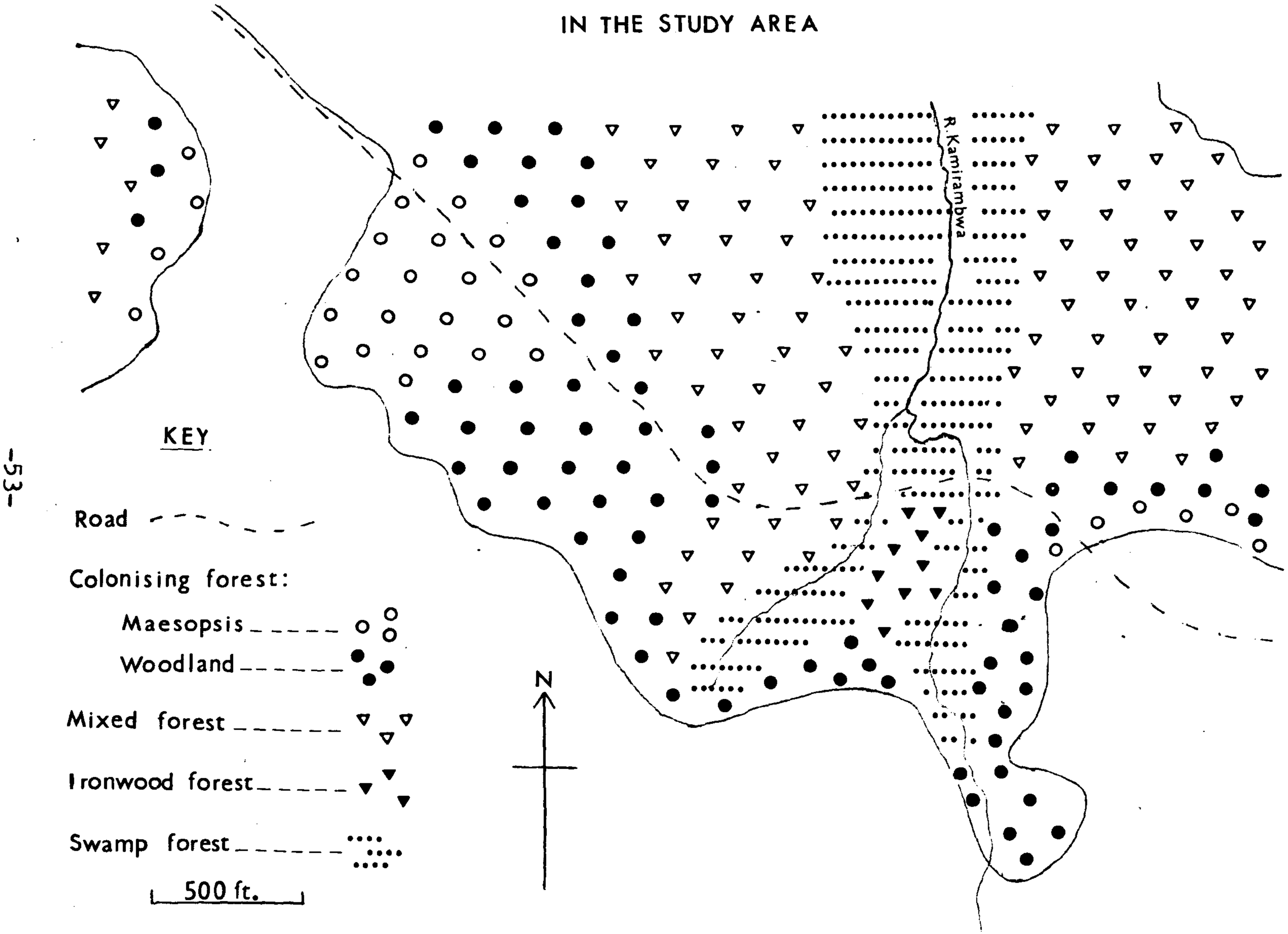
The whole region is described as mixed forest on Forest Dept. 1:30,000 forest type maps, but it contains a greater variety of forest types than this would suggest (see fig. 1.14). The western edge of the region is almost pure Maesopsis eminii, with a few Olea welwitschii and Funtunia spp intermingled. Elsewhere this is replaced by woodland colonising forest, containing Albizzia spp, Cordia milleni, Cola gigantea, Croton machrostachyus, Funtunia spp, Celtis spp, and young Khaya anthotheca, together with a few Maesopsis. Both these zones contain open spaces, choked with a dense growth of a bramble-like Rubus sp, or in shadier localities with Marantochloa leucantha. A very fierce small black ant builds its nests in the foliage and swarms everywhere in such clearings. Further from the forest edge the canopy becomes more continuous, and species such as Khaya anthotheca, Entandophragma spp, Mildbraediodendron excelsum,

FIG.I.II Aerial view of the study area.

FIG.I.I2 The road at the western end of the study area, where the canopy is continuous.

FIG. I.I3 The road at the eastern end, where it passes through swamp forest. Note the palm trees, Phoenix reclinata, in the valley bottom.

FIG. 1.14 DISTRIBUTION OF FOREST TYPES
IN THE STUDY AREA



Aningeria altissima, Trichilia prieuriana, Chrysophyllum albidum and Chrysophyllum perpulchrum predominate, along with a few Cynometra alexandri and a variety of Ficus spp. Yet deeper into the forest, and along the valley of the river Kamirambwa, Cynometra becomes more frequent, and in one place there is a small pure stand. Pseudospondias microcarpa grows in the swampy parts of this valley.

Most of the forest edge is surrounded by elephant grass, which attains a height of ten feet or more and makes it difficult to walk along outside the forest and observe monkeys on its edge, other than early in the year after the grass has been burnt. Exdeptions to this are a stretch of 150 yards at the western end of the area, where shorter grass predominates, and a small part of its southern edge where it is bordered by a coffee plantation. Short stretches of other parts of the forest edge can, however, be surveyed by climbing strategically situated termite mounds in the grassland.

That part of the study area that lies to the east of the river Kamirambwa falls within a region 4 sq. miles in extent set aside by the Forest Dept. as a nature reserve, in which no interference with the natural vegetation is permitted. Some timber was cut

in the remainder of the area during the early years of exploitation, and young Khaya anthotheca were planted there, but few of these appear to have survived. In 1957-1958 a few 'weed' trees that were damaging valuable timber trees were eliminated, but to date the area has not been extensively treated with arboricides. The vegetation is thus not unduly dissimilar to natural virgin forest.

STUDY METHODS AND DIFFICULTIES.

The detailed study of any animal presents its own peculiar problems, and the blue monkey is certainly no exception. The main difficulty lies in seeing the animals at all. In parts of the forest where the canopy is thin enough for monkeys to be clearly visible, the undergrowth below is so thick that it can be penetrated only by cutting (see fig. 1.15); the human observer can progress only at about 100 yards an hour, which is a lot slower than a startled monkey. Conversely, in places where the canopy is sufficiently dense to suppress the undergrowth, it is so thick that one cannot see anything in it anyway (see fig. 1.16). There are intermediates between these two extremes, but conditions of observation are seldom better than indifferent.

FIG. I.I5 A clearing in the Maesopsis forest at the western end of the study area. Note the dense layer of vegetation at ground level.

FIG. I.I6 Looking up into the dense canopy of mixed forest in the central part of the study area.The large trunk on the right is a mahogany, Khaya anthotheca. Note the lack of side branches for the first I00 ft.

This affects the collection of data in several distinct ways. Firstly, the time spent in contact with the monkeys is less than it would be in open country. The animals are difficult to find, and even when they are located it is often impossible to follow them for any distance should they start to move. As they are in contact with the observer only for short periods they become habituated relatively slowly. Long periods of observation are rare; a total of more than 2½ hours in a day was unusual, and some days went by without any observations at all.

Secondly, the poor visibility affects the quality of the data obtained. At any one moment it is seldom possible to see more than half the monkeys known to be in the area, and many of those visible might be partially concealed by foliage or branches. At the simplest level this means that many observations are fragmentary or incomplete. For instance, of the 517 grooming interactions recorded in the course of the study, the sex and age class of both participants was determined in only 250. At a more complex level it can lead to considerable difficulties of interpretation. The relation between what is seen and what is actually happening is never entirely clear, and initial impressions can be highly misleading. Counts of group

size and composition, for example, if taken at face value, can give a totally erroneous picture of social organisation. Likewise as Chalmers (1967, 1968a,b) has pointed out, some types of activity and certain sex and age classes may be more readily visible than others. Monkeys that are moving around, playing, or chasing will be more conspicuous than ones that are sitting about doing nothing or indulging in some less vigorous social activity such as grooming. Similarly certain sex and age classes might be more conspicuous than others by virtue of differences in size or behaviour. Behaviour recorded by the observer may therefore be a biased sample of the total behaviour of the animals. Such a bias is probably present to some extent in all field studies, but it is exaggerated in forest work because the screening effect of the environment is superimposed upon and reinforces the natural 'filter' of the observer. These problems are discussed at length in later chapters.

Since most of the difficulties of studying blue monkeys stem from the poor visibility in the forest, the would-be observer must devise some means of improving the conditions of observation. The most useful approach was found to be the cutting of an

extensive network of tracks (see fig. 1.17). This rendered possible silent and comparatively rapid movement throughout the study area. No attempt was made to establish a regular grid; rather the tracks were cut so as to give the greatest increase in visibility. Near the forest edge most were cut through the middle of clearings, and thus afforded an excellent view of the surrounding canopy. In places where the canopy was thicker, the tracks did not make so much difference to visibility, but made it easier to move about and provided useful fixed points of reference. Full use was also made of animal tracks in the area.

In theory visibility can be improved by climbing up into the trees. From as little as 20 ft. above the ground the view of the surrounding canopy may be greatly enhanced. This is clearly shown by the pair of photos in fig. 1.18, one of which is taken from ground level and the other from a few yards back from the same spot but 20 ft. up. In practice it is seldom possible to climb to any height as the larger trees have no branches for the first 80-100 ft. and the habit of growth of even the smaller trees makes their ascent difficult. Lianas appeared to offer a safe and easy route up into the canopy, but had a regrettable

FIG.1.17 TRACKS IN THE STUDY AREA

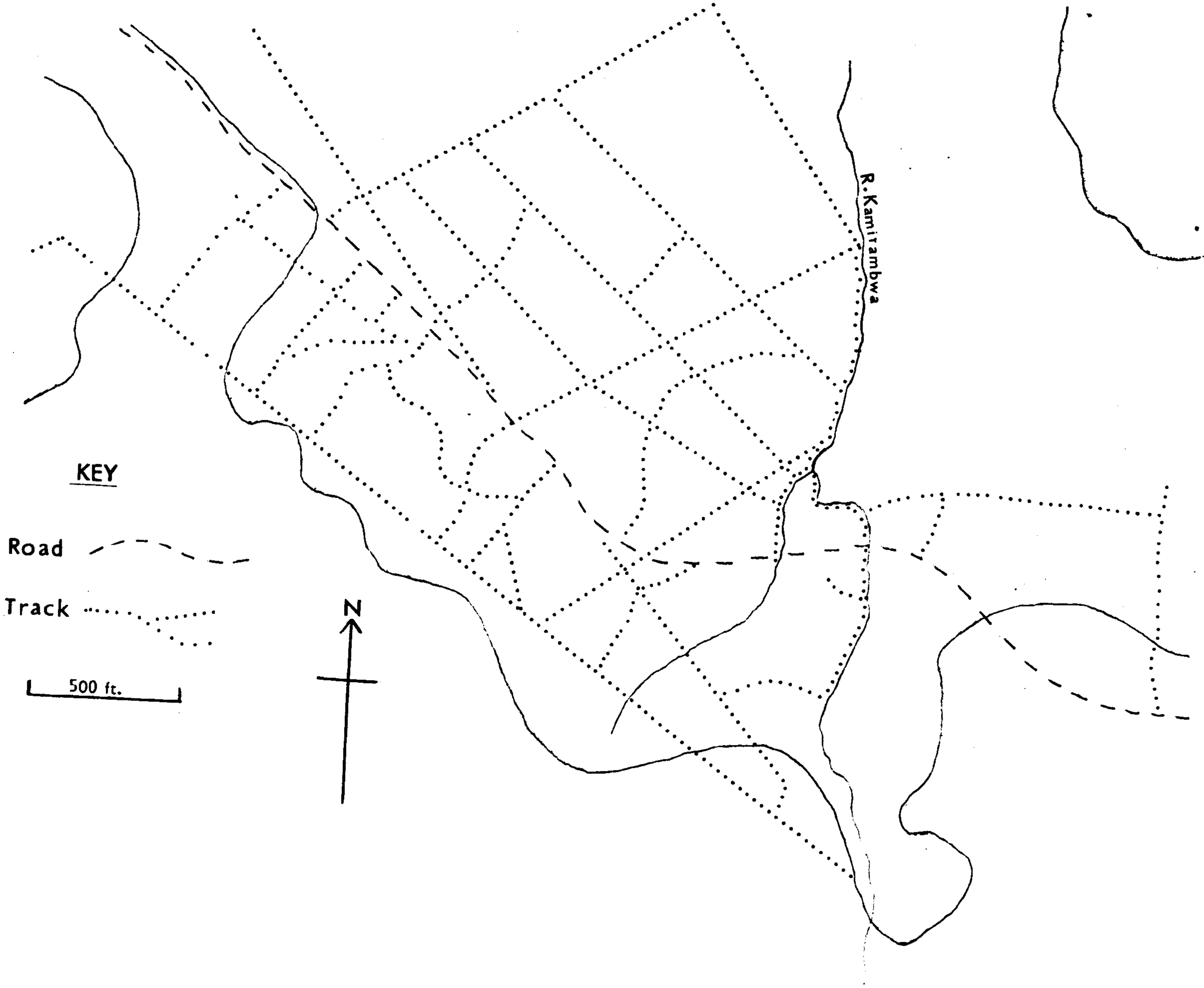


FIG.I.I8 Two views of the same area of mixed forest, one from ground level and the other from 20 ft. up.

tendency to break, or become detached from the branches. The building of permanent hides high in the canopy was considered, but it was decided that their usefulness would be too limited to justify the considerable difficulties involved in their erection.

The main method used in studying the monkeys was simply direct observation. If I knew the approximate sleeping position of a party of monkeys I would go there at first light and attempt to remain with them as long as possible thereafter, but if the animals had not been followed until dusk the day before the area was searched systematically, concentrating particularly on those regions known to contain food, until monkeys were located. In the early stages of the study it was found to be more productive to move on and look for another party of monkeys if contact with the original party was lost, but later on when they became tamer attempts were made to remain with the same animals throughout the day.

Direct observation is clearly the only way to obtain detailed behavioural data, and it also yields much information of other types. Initially, however, it was thought that topics such as population density and seasonal movements might more readily be investigated by running a series of strip censuses,

and an extensive program to cover all vegetational types at fortnightly intervals was planned. Censuses were found to be exceedingly time consuming; to be effective they had to be carried out in the early morning or late evening, the only parts of the day when monkeys were readily visible, so the time available for other observations was greatly reduced. Also it soon became clear that large scale movements of monkeys were infrequent or non-existent. Therefore the original program was drastically reduced; only two censuses were continued, and the intervals between censuses were greater and less regular. Details of method and results are discussed in Ch. 8.

I attempted to behave in such a way as to be regarded by the monkeys merely as part of the habitat. I tried to be as unobtrusive as possible, by wearing clothes of a colour that merged with the surrounding vegetation and avoiding the making of noises or sudden movements. On the other hand when monkeys were located they were approached slowly and quietly but no special care was taken to remain hidden from them. No efforts were made to 'provisionise' the monkeys in the Japanese manner. While this method may be of value under certain circumstances there is the risk that it may alter fundamentally their behaviour and social organisation.

Initially the monkeys would flee at distances as great as 100 yards, but after a few weeks they came to tolerate me within 30 yards or so and by the end of the study they would come as close as 20 ft. Most observations were made at a distance of 100-200 ft.

A pair of Ross 12 X 50 binoculars were used throughout the study. Photos were taken with an Asahi Pentax Spotmatic camera with a Novoflex 400 mm. follow-focus telephoto lens. This lens proved well suited to the difficult conditions, as it is very light, does not require a tripod, and can be focused rapidly. Sound recordings were made with a Uher 4000 Report-L tape recorder. All notes were taken in writing, during or immediately after the events concerned. Whenever possible records of behavioural interactions were transcribed onto file cards, certain types of data tabulated quantitatively, and sightings and movements of monkeys plotted on a map of the study area the same evening.

Chapter 2

POPULATION STRUCTURE

THE PROBLEM OF POPULATION STRUCTURE.

Most monkeys and apes that have been studied to date live in well defined social groups. These vary in their size and composition, and the basic units may sometimes be combined into larger aggregations (e.g: geladas, Crook 1966, hamadryas baboons, Kummer 1968), but there is seldom any difficulty in establishing the existence of such groups. The only major exception is the chimpanzee. Chimps are found in small parties* of varying composition that join together and split up again depending on feeding conditions (Reynolds and Reynolds 1965, Goodall 1965, 1968). In forest habitats parties may be drawn from 'regional populations' of 30-60 animals, each having a well defined home range (Sugiyama 1968b), but if such higher levels of organisation exist they are not closed social units and hence not strictly comparable to the groups of other species.

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* In this dissertation the term 'group' is used to denote the basic social unit of a species. 'Party', on the other hand, refers to an aggregation of animals of uncertain social status; for example a party might be a small portion of a group, or two groups combined.

In the blue monkey a discrete group structure is not immediately apparent. The monkeys are generally encountered in small parties of perhaps four or five animals, but these parties are seldom compact and well defined. They may coalesce or split up, and there appears to be little constancy in their composition from day to day. Recognisable individuals are seen sometimes together and sometimes in separate parties up to $\frac{1}{4}$ mile apart. This apparent lack of constancy in dispersion is illustrated in fig 2.1 (a-g), in which the composition and movements of all parties of monkeys encountered on seven successive days are plotted on maps of the study area. While there is a tendency for monkeys to be seen in the same place from day to day, the numbers vary greatly. For instance on each day during this period monkeys were seen to visit a flowering Albizia tree to the north of the road to feed, but the numbers doing so varied from 3 to 14.

A further illustration of such variability is given in fig. 2.2, showing the composition of parties containing a recognisable female on each occasion that the animal was sighted. Here again there is considerable variation.

At first sight, therefore, the blue monkey pattern

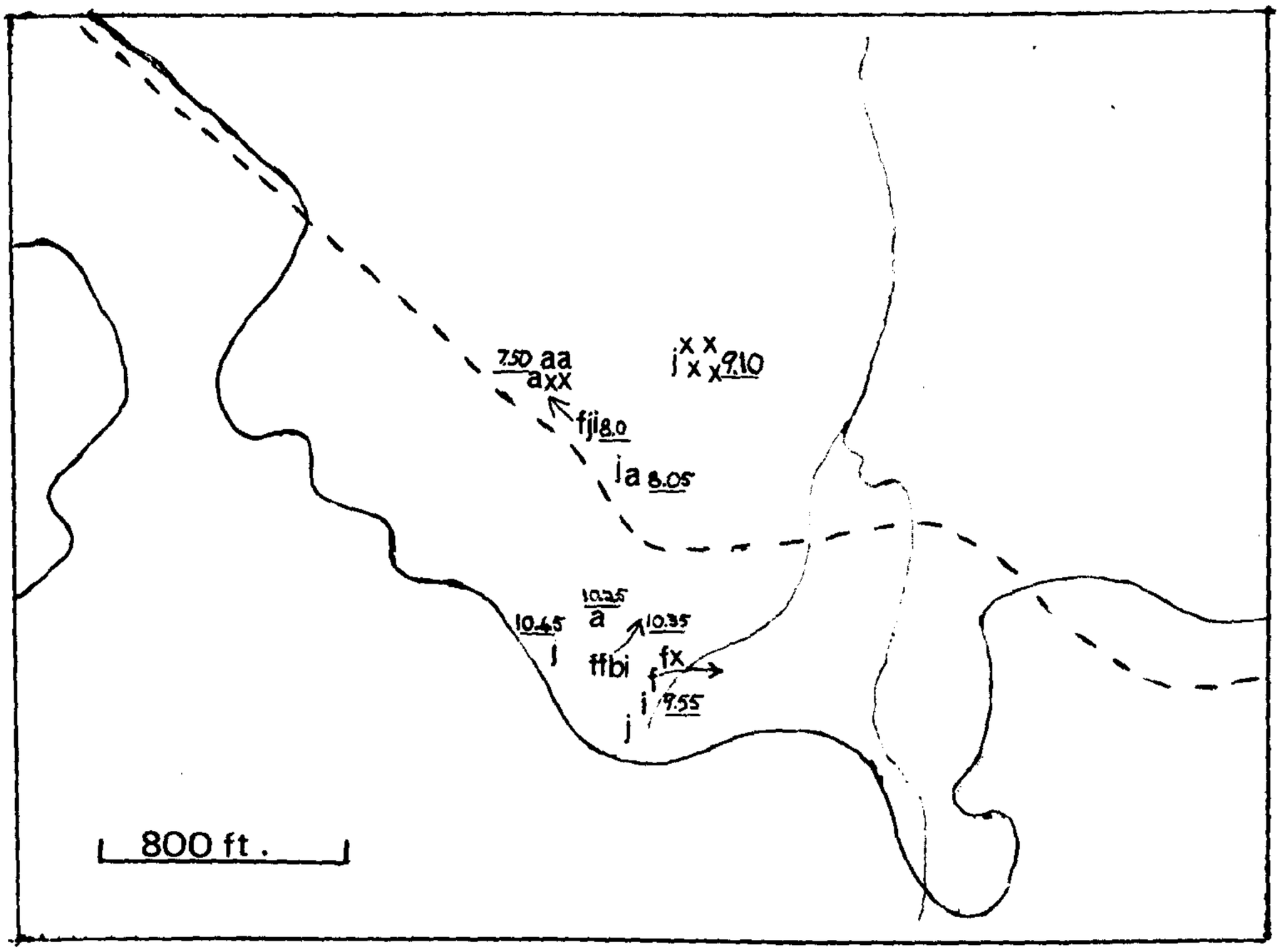
of social organisation appears to be rather similar to that of the chimpanzee. But can this initial impression be taken at face value? It is possible that the apparent lack of well defined groups might result from the restricted visibility in the forest. If a group of monkeys were spread over an area greater than the observer's field of vision one would expect to see only a small proportion of them at any one moment. This then is the critical question; is there in fact no definite group structure, or is the apparent lack of discrete groups an artifact of the conditions of observation?

Data on the apparent size and composition of parties were subjected to critical analysis to try to determine the causes of variation. Firstly, it was found that the apparent size of parties increased progressively with time after the initial sighting. This phenomenon is illustrated in fig. 2.3, based on 106 encounters with monkeys in the study area during three ten day sample periods, 5/6/66 - 14/6/66, 23/10/66 - 1/11/66, and 15/1/67 - 24/1/67. It will be seen that while the average number of monkeys <u>actually visible</u> remains relatively constant, the 'apparent party size', that is the number <u>known to be in the vicinity</u> of the observer, increases steadily.

FIG. 2.1

SIGHTINGS AND MOVEMENTS OF MONKEYS IN THE STUDY AREA

(a) FEB. 7th. 1967



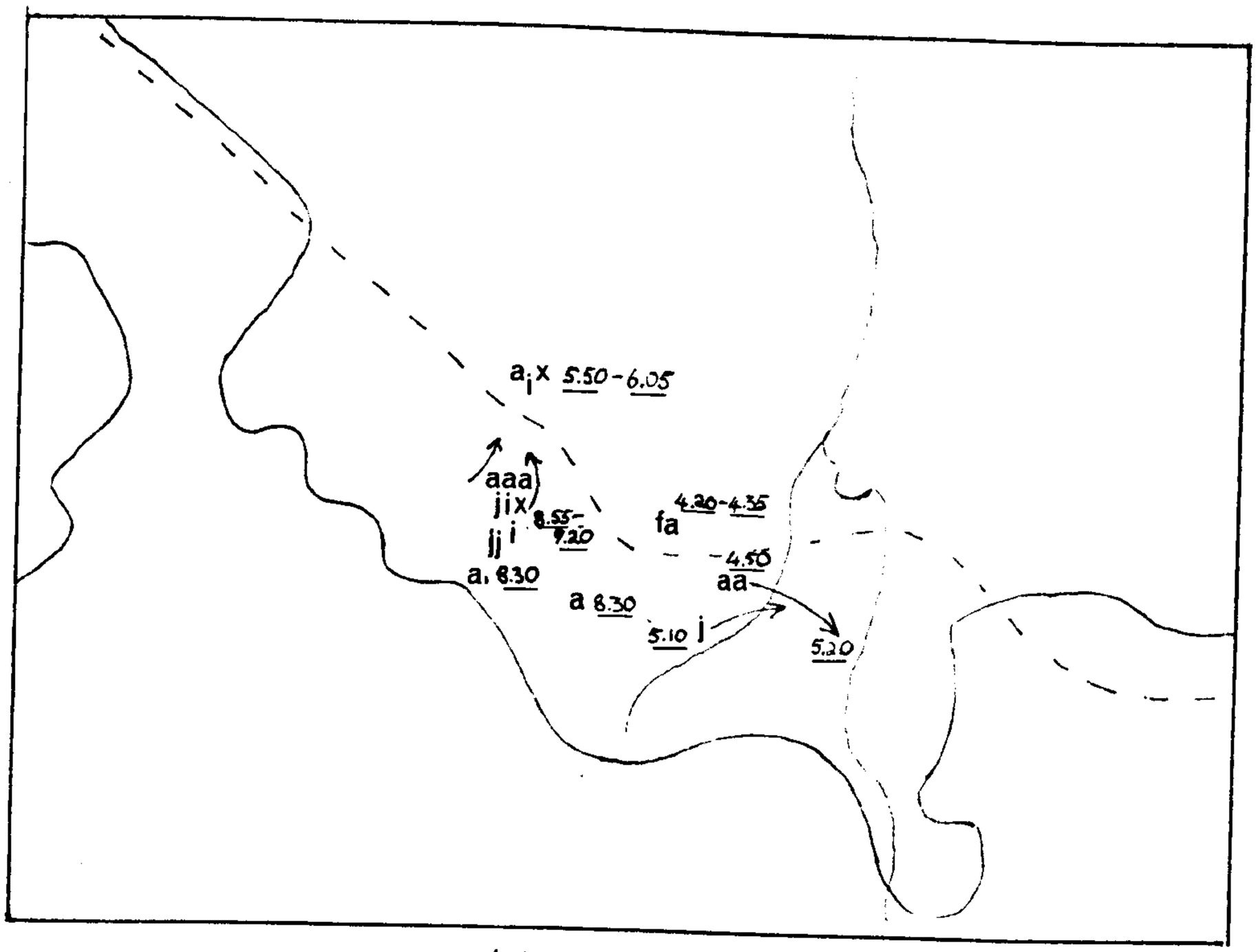
KEY

m__male
f__female
a__unsexed adult
j__juvenile
i__infant
b__baby
x__unclassified

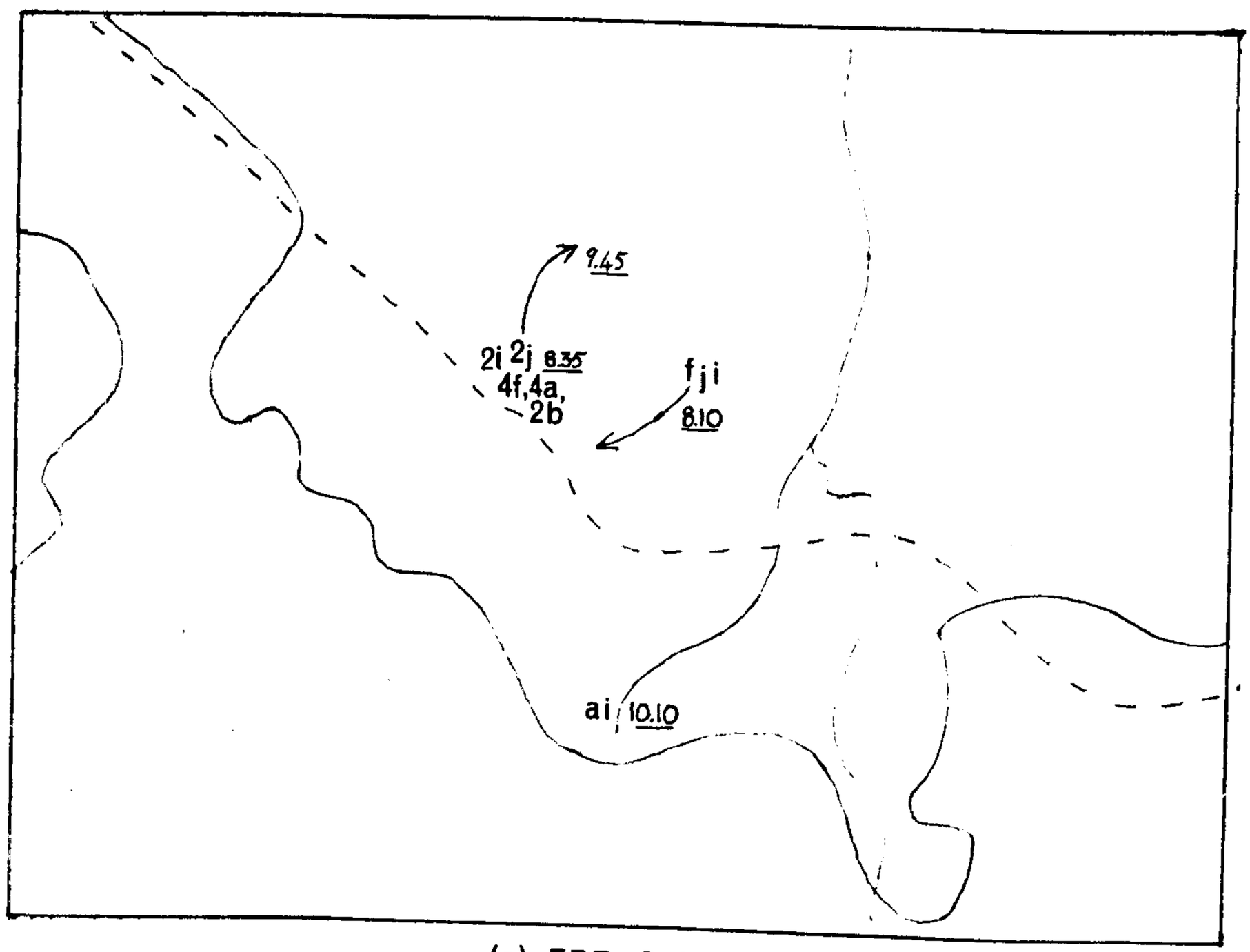
Underlined numbers refer to times

Arrows denote direction of movement

FIG. 2.1 (cont)

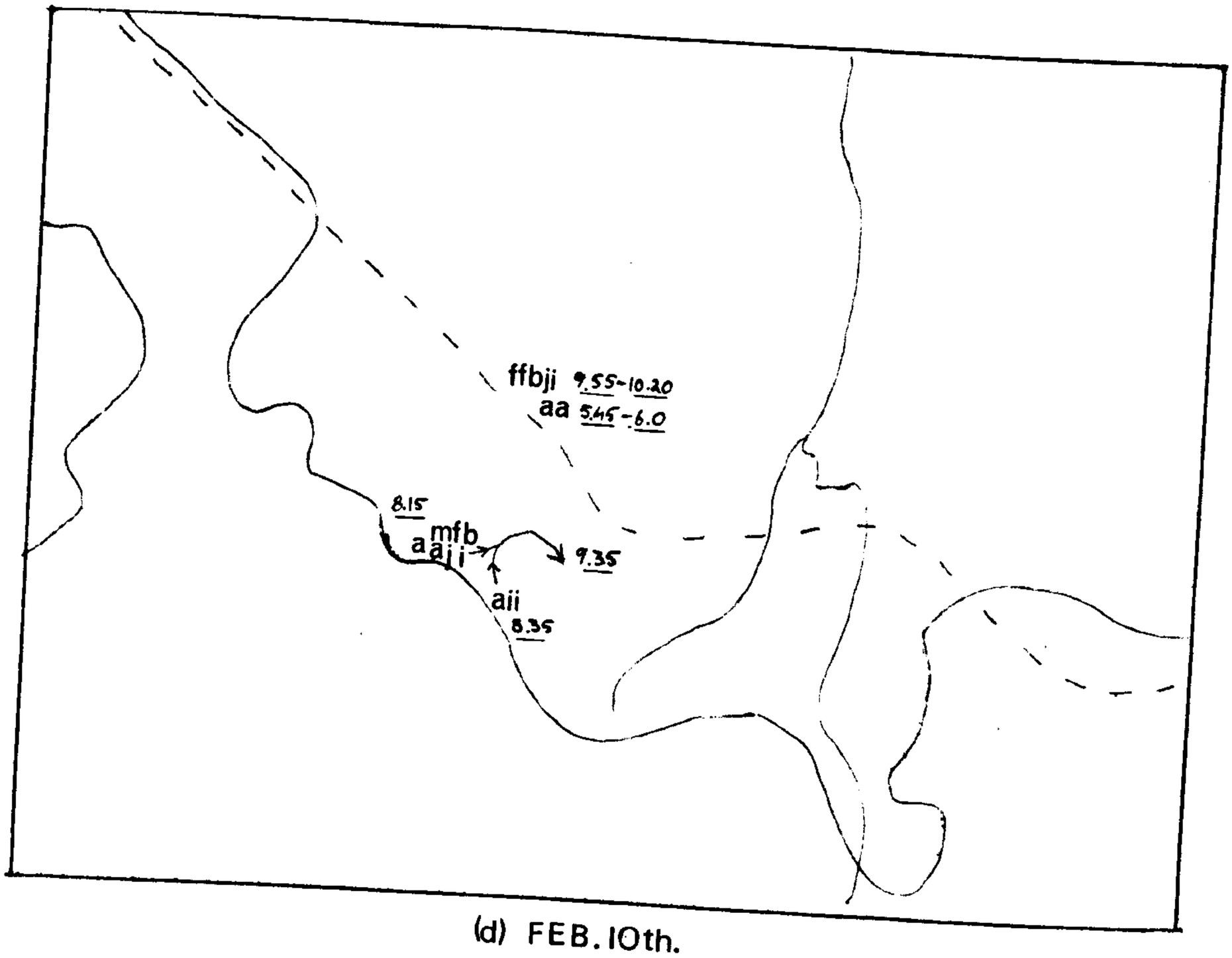


(b) FEB. 8th.

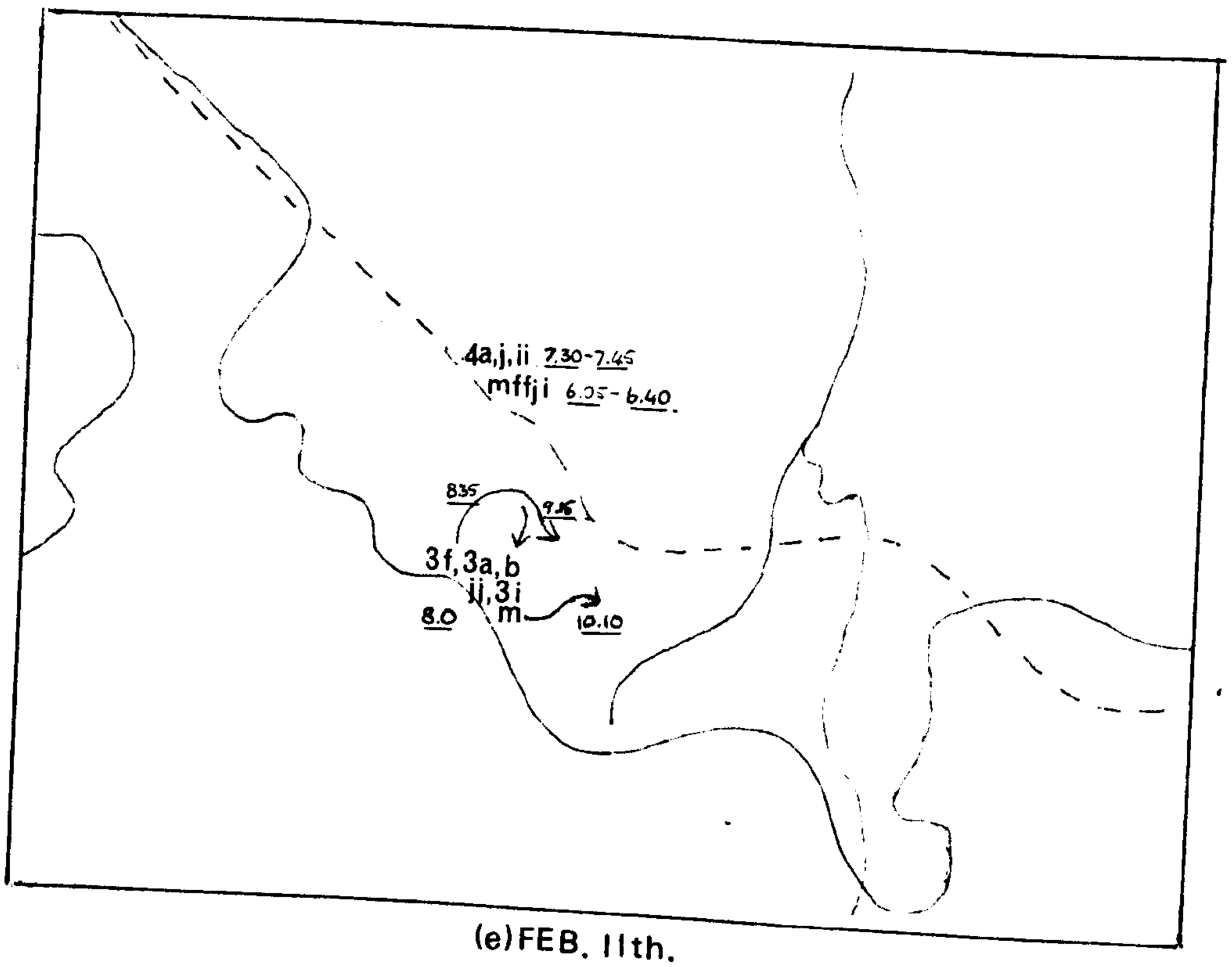


(c) FEB. 9th.

FIG. 2.1 (cont)

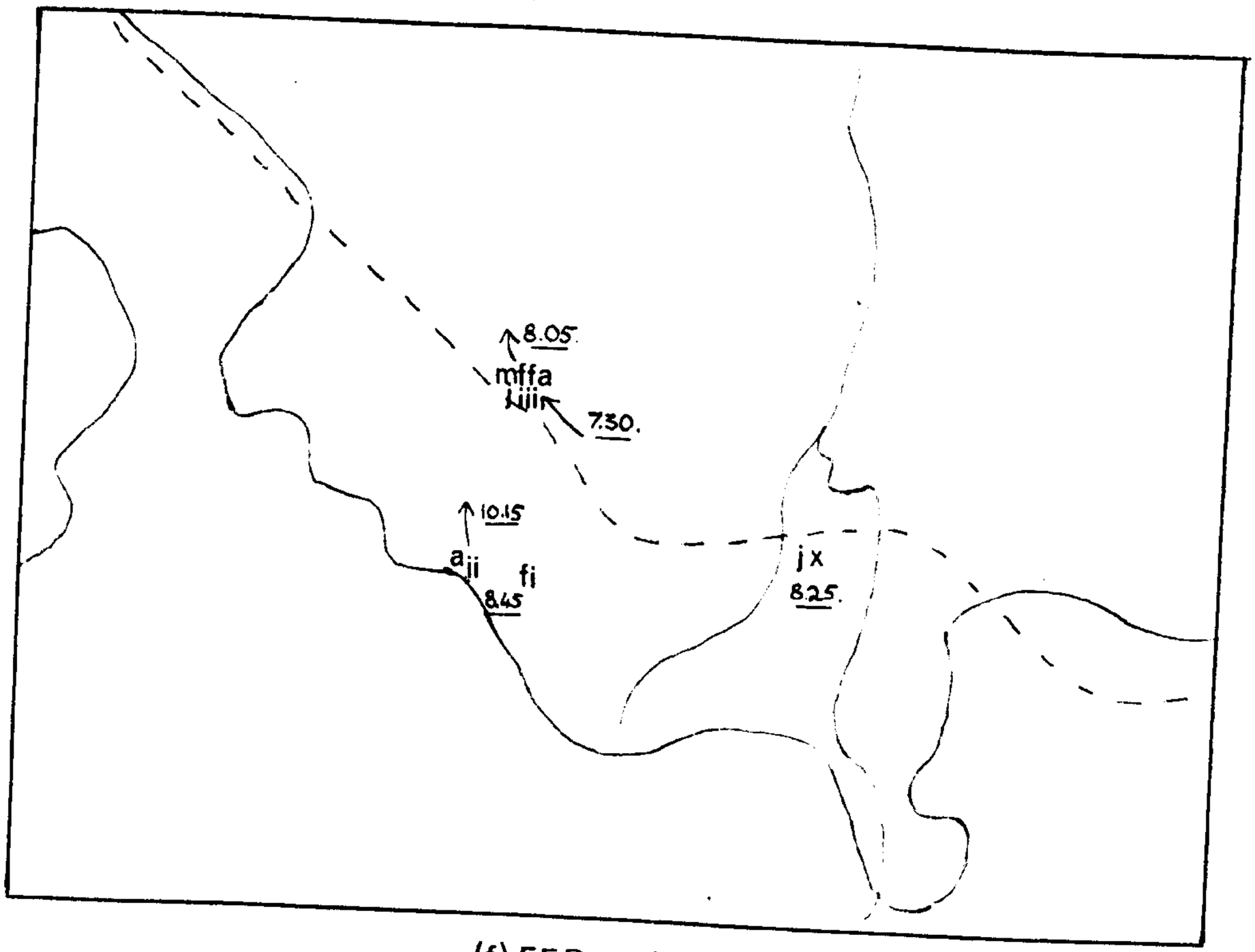


(d) FEB. 10th.

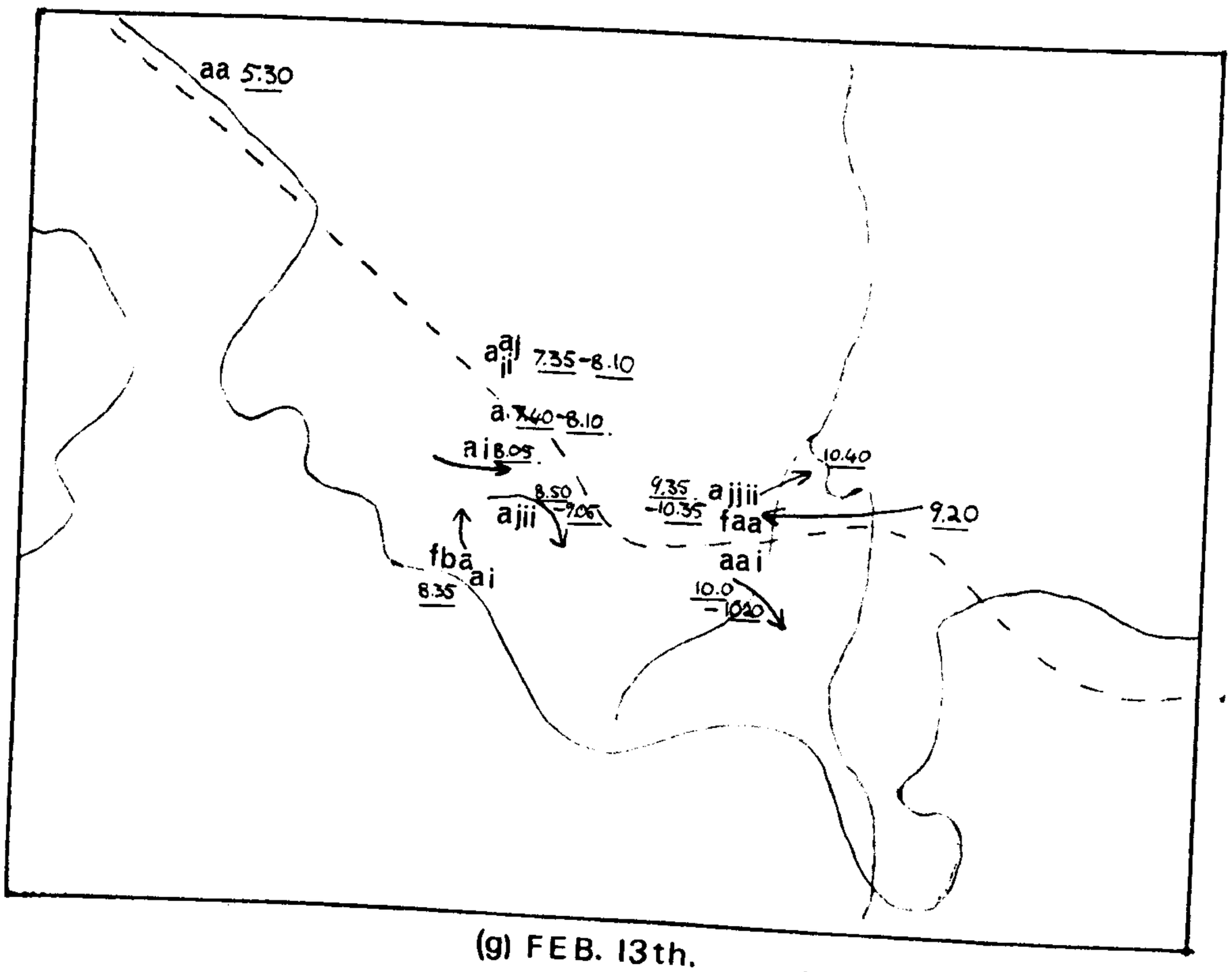


(e) FEB. 11th.

FIG. 2.1 (cont)



(f) FEB. 12th.



(g) FEB. 13th.

FIG. 2.2 Composition of parties containing a recognisable female.

Date	mature male	young male	female	unsexed adult	juv.	infant	baby	Others	TOTAL
6/7/66	-	-	I	-	I	-	-	-	2
7/7/66	-	-	I	2	I	I	-	-	5
27/7/66	I	-	2	I	I	3	I	-	9
3/8/66	I	-	2	I	I	I	I	3	IO
4/8/66	I	-	2	-	-	I	-	-	4
8/9/66	-	-	I	I	-	3	-	-	5
7/IO/66	-	-	I	I	I	-	-	-	3
8/IO/66	-	-	2	-	3	4	-	-	9
IO/IO/66	-	-	I	I	-	I	-	-	3
IO/I2/66	I	I	2	I	2	I	I	-	9
2I/I/67	I	-	3	3	2	2	-	-	II
23/I/67	I	-	2	3	I	3	2	-	I2
24/I/67	-	-	4	I	-	3	-	I	9
I4/2/67	-	-	I	-	-	-	-	-	I

FIG. 2.3

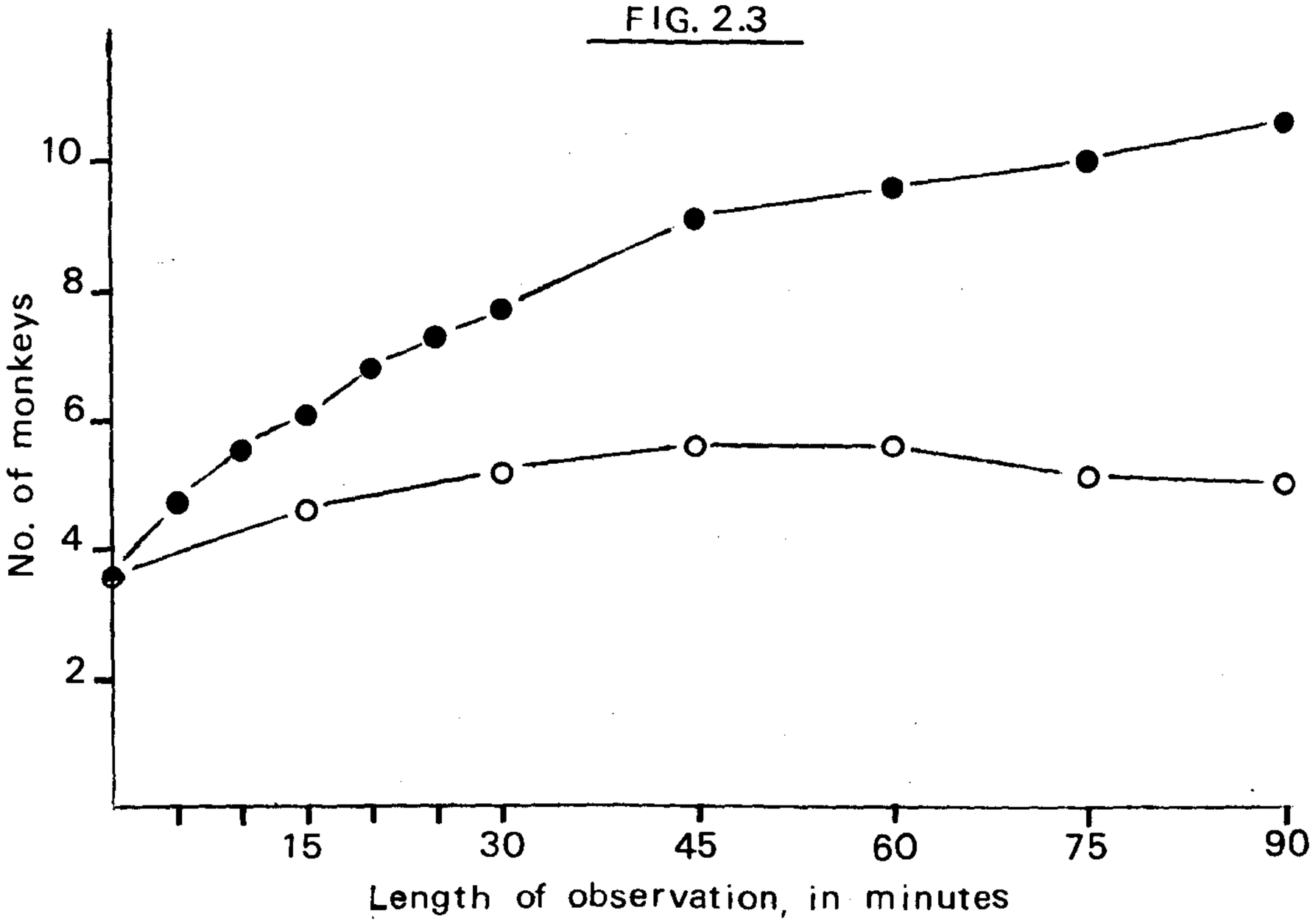
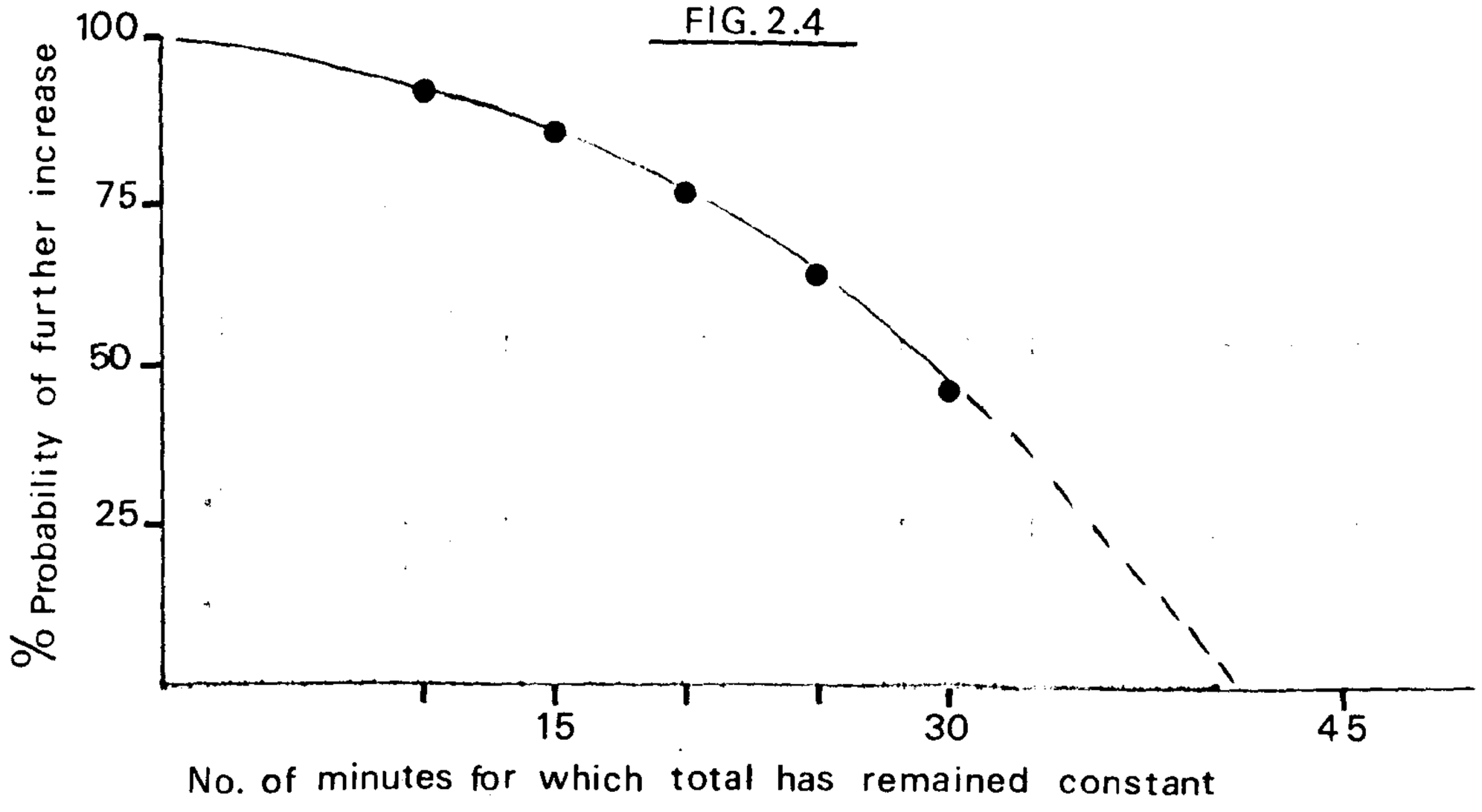

No. of monkeys
10
8
6
4
2
15
30
45
60
75
90
Length of observation, in minutes
● —— ● Apparent party size
○ —— ○ Number actually visible
(see text for explanation)

FIG. 2.4


% Probability of further increase
100
75
50
25
15
30
45
No. of minutes for which total has remained constant

The increase is at first rapid, and then slows down, but even after an hour's observation more monkeys may appear.

There are various possible causes of this increase in apparent party size. It could be due to monkeys that were partially concealed by foliage, and hence overlooked at first, subsequently being noticed by the observer. If this were so one would expect the increase in apparent party size to be matched by an increase in numbers actually visible. In practice the discrepancy between the two counts increases steadily. Only a small part of the rise in apparent party size can therefore be ascribed to improvement in observer efficiency. The remainder must be due to monkeys moving into the observer's field of vision from elsewhere, either from behind thick cover in the immediate vicinity or from some distance away. While it was not always possible to distinguish between these in the field, monkeys were frequently seen to approach from some way away. We may infer, therefore, that if the monkeys do live in distinct groups the groups are commonly spread over a distance greater than can be seen in forest.

Since visibility is so limited, this conclusion is not in itself particularly surprising, but it does

have important consequences. Most periods of observation are short, 30-40 minutes or less, so one will seldom have seen all the monkeys in the vicinity before contact is lost. Counts of apparent party size will therefore be misleading if taken as representative of group size.

This would not be such a serious drawback were it possible to predict the actual number of monkeys present, given that a certain proportion of them had been seen in a short time. If there was little variation in the 'growth rate' of parties after the initial sighting this would be possible, but unluckily there is too much variation in the rate of increase for such an approach to be feasible.

An alternative method is to determine the number of cases in which apparent party size increases further after being constant for various lengths of time. It might be found, for instance, that if the apparent total remained constant for half an hour no more monkeys ever appeared, and one might then be justified in concluding that all those in the vicinity had been seen. Fig. 2.4. represents the result of analysing in this way all periods of observation of an hour or more obtained during the same three ten day sample periods. For example, of the 35 cases in which

apparent party size remained constant for 10 minutes, it increased further in all but three. The probability of further increase when the total has remained constant for 10 minutes is therefore $\frac{32}{35}$, i.e. 0.914. Similarly of the 28 cases in which the total remained constant for 30 minutes it increased further in 13; probability of further increase is hence $\frac{13}{28}$, or 0.464. Extrapolation of the curve, assuming for the sake of argument that it maintains the same form, indicates that it would meet the x axis at between 40 and 45 minutes. Hence the apparent total would have to remain constant for at least this long before one could be certain that no more monkeys were going to appear. In practice the total very seldom remains constant for as long as 45 minutes, so this approach is of little practical value.

The thickness of the forest is another factor that might be expected to affect the numbers of monkeys seen. The canopy was too heterogenous to permit an accurate assessment of all-round visibility in different parts of the s tudy area, so counts of apparent party size cannot be related directly to visibility. However the apparent spread of each party, that is the distance between the two most widely separated individuals, was estimated. The correlation between apparent size and spread was therefore

investigated, using data from the same three sample periods. In order to eliminate variations in party size resulting from different lengths of observation figures for apparent size and spread after 15 minutes were used. The choice of 15 minutes seems a reasonable compromise between a time so short as to render counts of party size highly unreliable and one so long as to eliminate much of the data; of the 106 parties encountered during the sample periods only 78 were watched for 15 minutes or longer, and only 53 for 30 minutes or longer. Disregarding three encounters with solitary animals, we are left with 75 paired observations of apparent party size and spread (see fig. 2.5). These yield a correlation coefficient (r) of 0.31. The probability of obtaining a value differing from zero by this much in either direction is less than 0.01, so we may safely conclude that there is a weak but positive correlation between the apparent size of a party of monkeys and the distance over which it is spread. Since the larger spreads recorded are far greater than the typical range of visibility, it seems reasonable to conclude that the thickness of the forest will affect the number of monkeys seen.

Another factor that might perhaps influence

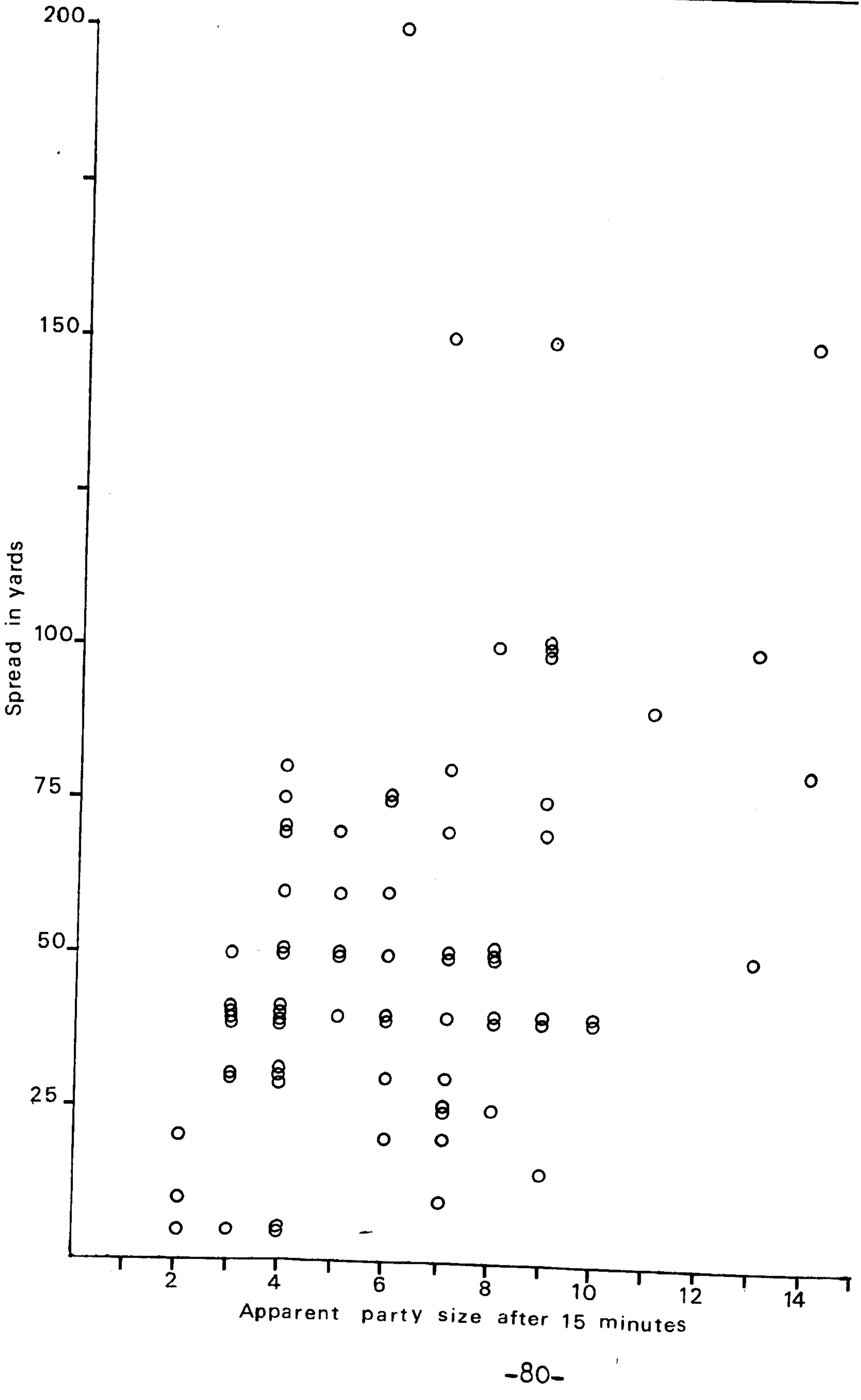
apparent party size is the time of day. Buxton (1952) claimed that parties of Cercopithecus ascanius varied in size during the course of the day, small sleeping parties joining up in the early morning to feed, separating again for the mid-day rest period, forming larger aggregations again in the afternoon, and dividing up once more at dusk. Buxton's conclusions can be criticised on statistical and other grounds (Struhsaker 1969, Aldrich-Blake 1970), but the possibility of such variation in the blue monkey must nevertheless be considered.

My subjective impression was that parties of blue monkeys do indeed appear to be smaller in the middle of the day. Below are shown the mean apparent sizes after 15 minutes of parties encountered during each hour of the day, in the same three sample periods, together with numbers of parties for each hour.

Time	6-7	7-8	8-9	9-10	10-11	11-12	12-1
Av.size after 15 mins.	8.5	8.25	5.5	4.8	4.9	5.0	9.0
No. of parties	2	16	13	7	7	3	1

Time	1-2	2-3	3-4	4-5	5-6	6-7
Av.size after 15 mins.	8.0	-	6.4	5.6	4.2	6.75
No. of parties	1	-	7	8	9	4

FIG. 2.5 RELATION BETWEEN PARTY SIZE AND SPREAD



If the two high values, based on single parties, for the middle of the day are disregarded, the figures suggest that party size diminishes between dawn and mid-day and rises again in the afternoon. This pattern should be treated with suspicion, however. Since the monkeys are inactive during the night one would expect average party sizes for dawn and dusk to be similar; in practice the discrepancy between them is almost as great as that between the figures for dusk and the lowest values in the late morning.

To facilitate statistical analysis parties were divided into two size categories, from 1 to 6 individuals, and 7 or over. (The mean size of the 78 parties is 6.1, and the median is 6). The frequences of small and large parties during each hour of the day are as follows:

Time	6-7	7-8	8-9	9-10	10-11	11-12	12-1
1-6	1	4	8	6	5	3	-
>6	1	12	5	1	2	-	1

Time	1-2	2-3	3-4	4-5	5-6	6-7
1-6	-	-	3	5	7	2
>6	1	-	4	3	2	2

A Kendall's S test fails to reveal any significant trend ($z = 1.17$, $p = 0.242$). The initial impression

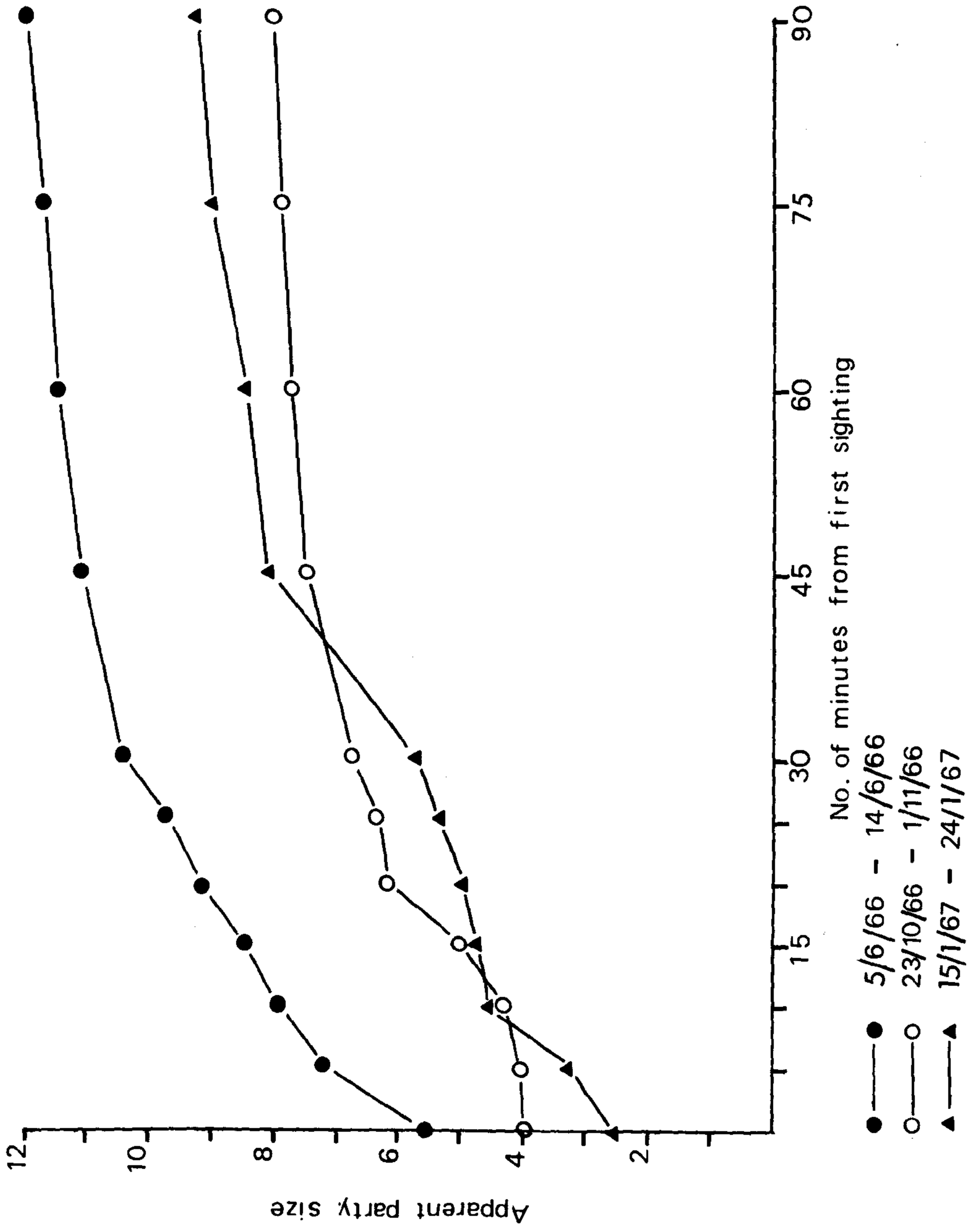
that apparent party size is low in the middle of the day and high in the early morning and evening is hence not confirmed.

Careful observation indicates that if any such trend existed it would result not from actual splitting and coalescence of parties, but from the difficulty of seeing monkeys during the heat of the day when they become inactive and retreat into thick foliage. The average number of monkeys actually visible declines during the middle of the day, particularly in the dry season; hence it would take longer to see all those in the vicinity and a smaller proportion would have been noticed during the first 15 minutes observation.

While party size appears to fluctuate but little from one time of day to another, there remains the possibility of changes on a longer time scale, say of days or weeks. In fig. 2.6 increase in mean apparent party size with time is plotted for each of the three sample periods separately. Means for the period 5/6/66 - 14/1/66 appear consistently higher than those for the other two samples. The raw data from which the means for apparent size after 15 minutes were calculated were compared by Mann-Whitney U tests with corrections for ties. It was found that apparent

FIG.2.6

INCREASE IN APPARENT PARTY SIZE WITH TIME



party sizes for the sample periods 23/10/66 - 1/11/66 and 15/1/67 - 24/1/67 do not differ significantly ($p = 0.7188$), but both these are significantly different from the period 5/6/66 - 14/6/66 ($p = <0.0006$ in each case, two tailed). Similar results were obtained when apparent party sizes after 30, 60 and 90 minutes were compared.

Since the apparent size of parties is affected by the thickness of the canopy it could be argued that these differences are due merely to seasonal changes in visibility from one sample period to another, or that most of the observations during the period in which larger parties were seen happened to be made in a part of the study area where visibility was better than average. Comparison of the apparent spread of parties by the same method indicates that this is not the case; there are no significant differences between any one period and another.

What then are the underlying reasons for these long term changes in apparent party size? Differences in feeding conditions would appear to be the most significant factor. During the period 15/1/67 - 24/1/67 food was sparse and scattered. The forest was very dry and the main items of diet were buds and young shoots; trees bearing these were few and widely

dispersed, and the monkeys were commonly encountered in small parties. During the period 5/6/66 - 14/6/66 a few trees with heavy crops of fruit provided very concentrated sources of food, and large parties were seen. From 23/10/66 - 1/11/66 several species of tree were fruiting, and food was abundant almost everywhere. Under these conditions small parties were again the rule, even though any one tree contained enough fruit to feed a large party of monkeys. It would seem, therefore, that blue monkeys normally occur in small parties, but have the ability to form larger aggregations if feeding conditions so dictate. (The relation between feeding conditions and dispersion is considered more fully in Chapter 4). Thus while much of the apparent variation in party size is an artifact of the conditions of observation, some at least is a consequence of the monkeys' social organisation.

However, this does not bring us any nearer to determining what the basic social structure of the species is. Variation in party size with changes in feeding conditions might take place within an overall group structure, or on the other hand there might be no distinct groups. Initial impressions, during the first few months of the study, favoured the second

alternative, but subsequently patterns of behaviour were observed that seemed incompatible with such a system.

Examples of such incidents are as follows:

On the morning of 3/7/66 a party of 13 monkeys containing a recognisable female ('tuft-tail') moved out of the range in which this female had previously been seen into an area known to be inhabited by two other recognisable individuals. Neither of these animals had ever been seen in the same party as 'tuft-tail'. The area contained several Pseudospondias microcarpa with a very heavy crop of fruit; 'tuft-tail's' original range had no obvious source of food in it at the time. The party of 13 started to eat Pseudospondias fruits. When they had been feeding for 15 minutes there was a sudden outburst of harsh noises and violent movements in the foliage. Conditions of observation were as usual indifferent, but monkeys were glimpsed chasing one another. After a few seconds the original party rushed out of the Pseudospondias trees and disappeared the way it had come. A second party of monkeys remained in the fruiting trees. A mature male from the second party made loud 'volley calls' (see Chapter 5), and bounded through the canopy for some distance after the first party.

Similarly, on the evening of 7/6/66 a party of 10 monkeys was feeding in a fruiting Aningeria altissima. A second party of 10 or 12 monkeys approached this tree from one side, and as it did so the original party started to move out on the other side. The first members of the second party reached the Aningeria before all of the first party had left, and adults from the two parties threatened and chased one another. A mature male in the second party made loud volley calls, and a male in the first party answered him with similar noises. Both continued to call for three minutes, and a third male about $\frac{1}{4}$ mile away started calling also. After 5 minutes all of the first party withdrew, and the second party settled down to feed.

Such behaviour is in complete contrast to the invariably peaceful mingling of smaller parties. When

small parties coalesce the only overt behaviour is a few quiet croaking noises as they come into contact with one another. Threat and aggression are hardly ever seen outside the circumstances described above, even under the same sort of feeding conditions. It is tempting to conclude that such incidents are examples of territorial behaviour, and that the large parties involved represent distinct groups.

The 'volley call' made by mature males during these encounters is sometimes given at other times. It is one of the loudest of blue monkey noises, and can be heard at a distance of more than half a mile. It is given only by mature males, and if one male starts making it others up to a third of a mile away may answer. A similar interchange of loud calls has been described in other forest species ... the 'dawn chorus' of the howler monkey is the classic example (Carpenter 1934) ... all of them known to live in well defined groups and be territorial. (The significance of volley calls is discussed further in Chapter 5).

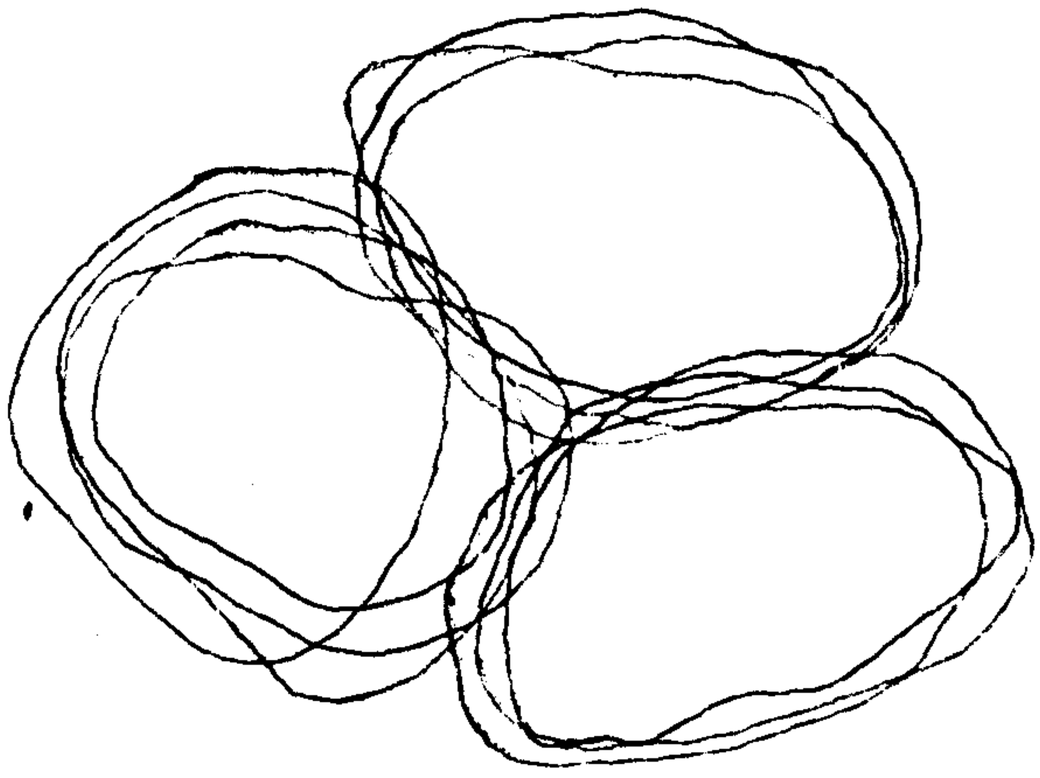
Further evidence relevant to the problem of population structure can be obtained from a consideration of the home ranges of recognisable individuals. If the monkeys lived in stable groups with well

defined home ranges overlapping only marginally with those of adjacent groups, one would expect the range of each individual to overlap greatly with that of any other member of the same group, but little or not at all with those of monkeys from other groups. In other words monkeys that were sometimes seen in the same party should have ranges that overlap to a much greater degree than those of individuals that were never seen together. Such a situation is represented diagrammatically in fig. 2.7 (a). If, on the other hand, there are no distinct groups one might expect the ranges of individual animals to show all degrees of overlap, as portrayed in fig. 2.7 (b). By mapping the home ranges of the few individuals that were recognisable for long periods it should be possible to gain some idea as to which type of social organisation prevails. If the home ranges approximate more closely to the situation shown in fig. 2.7 (a), we may conclude that the monkeys do indeed live in discrete groups with home ranges that overlap but little. If the position is more like that portrayed in fig. 2.7 (b), however, this could mean either that there is no definite group structure or that there are discrete groups but the groups' home ranges overlap to a large extent.

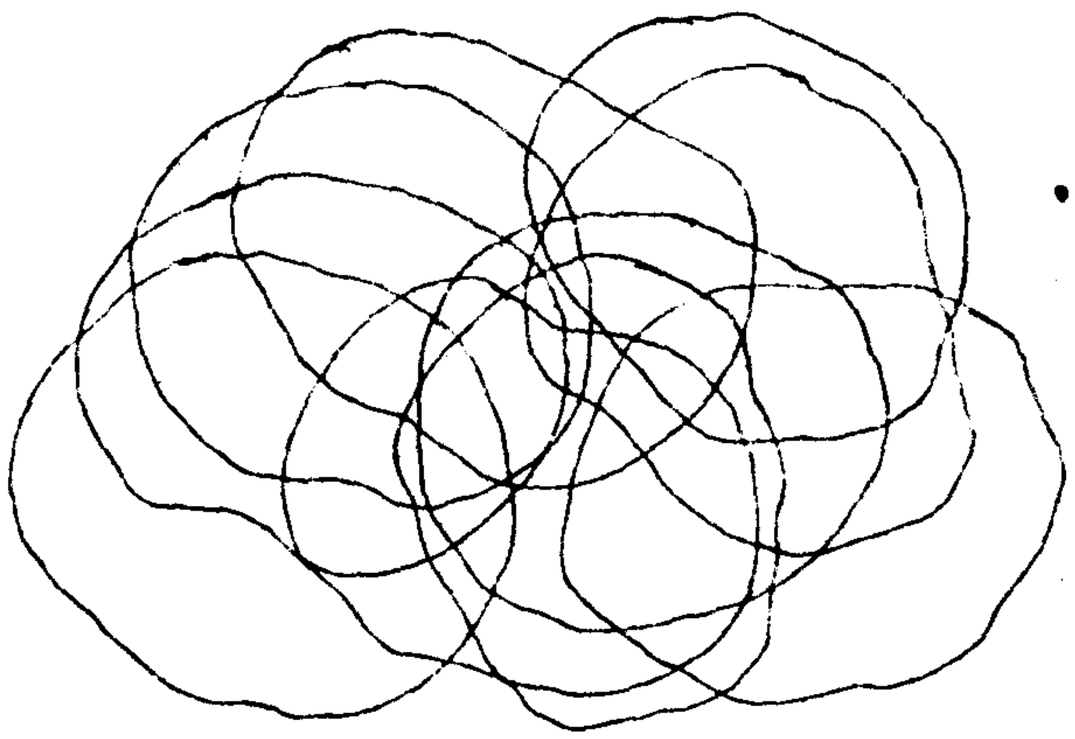
The home ranges of ten recognisable individuals that were seen on more than three occasions and distinguishable beyond all doubt were examined to see to which of the two alternatives they approximated more closely. All sightings and movements of these monkeys were plotted on maps of the study area and converted into home ranges by drawing straight lines round the outermost points. The 10 maps of individual ranges were superimposed to give fig. 2.8. It will be seen that the ranges form two sets of three and one of two with large overlaps, the remaining two overlapping to a moderate extent. The two overlapping ranges in the S.E. corner of the study area are of a female and her infant, which should perhaps be considered as a single unit, but even so the figure bears a greater resemblance to fig. 2.7 (a) than 2.7 (b). Moreover in the 8 cases in which pairs of ranges overlap to a large extent the individuals concerned were sometimes seen in the same party in all but two, and these two pairs were animals that were not recognisable during the same part of the study. Admittedly the number of recognisable animals involved is small, and since most were only distinguishable for short periods their ranges might be incomplete, but the results are nevertheless suggestive.

FIG. 2.7

Theoretical patterns of individual range overlap.



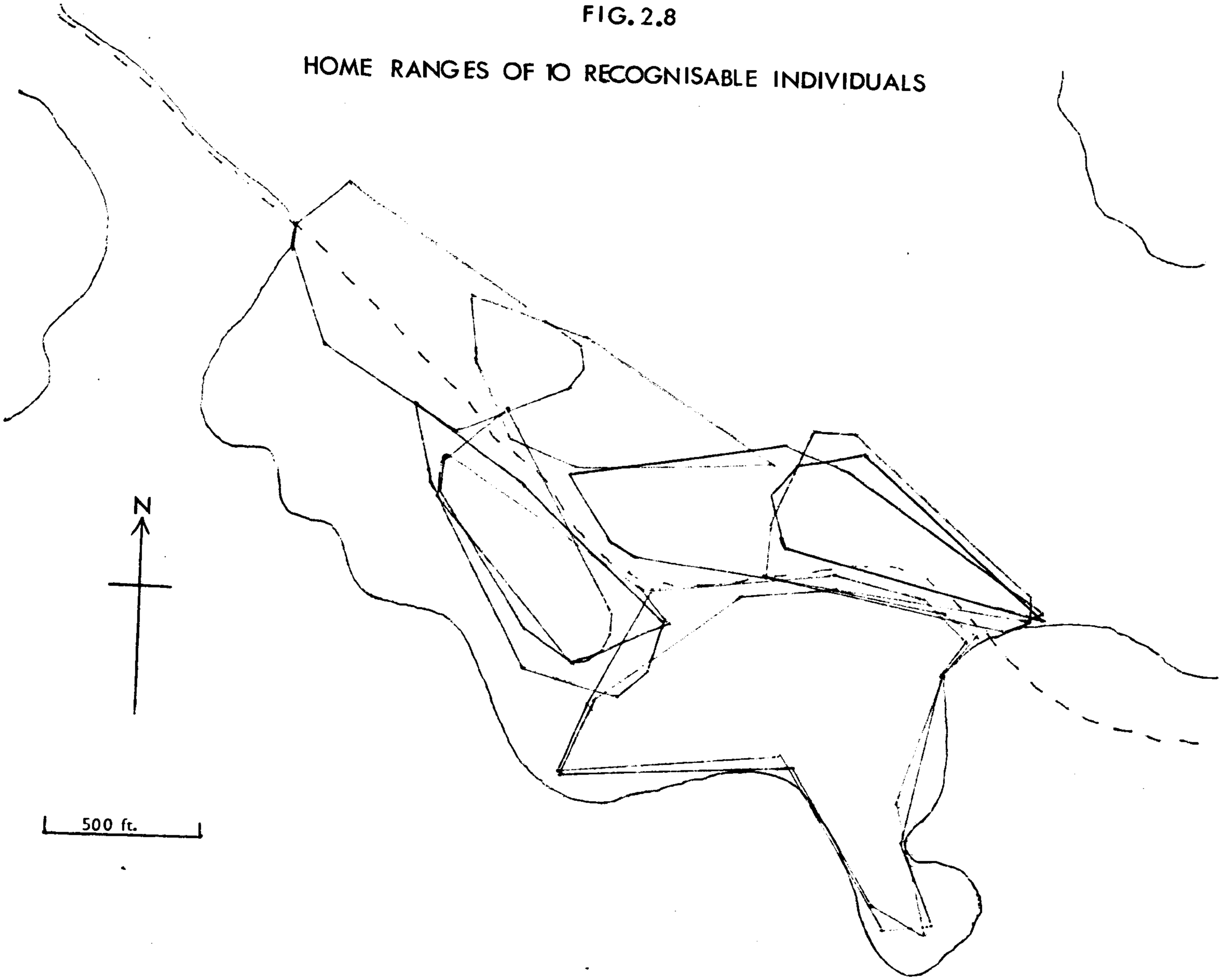
(a). Ten individual ranges in three sets, with marginal overlap between sets and large overlap within sets.



(b). Ten individual ranges with all degrees of overlap.

FIG. 2.8

HOME RANGES OF 10 RECOGNISABLE INDIVIDUALS



There is on the one hand, then, considerable flexibility in dispersion as revealed by changes in average party size with feeding conditions, and, on the other, evidence strongly suggestive of a division of the population into distinct groups. Any hypothesis of social organisation must be capable of accommodating both sets of facts. The most likely explanation would seem to be that blue monkeys do indeed live in distinct groups, but that the groups do not move as compact, integrated units. Under typical feeding conditions the group would be scattered over a wide area and individual parties might forage independently of one another. Only when food supplies were rich and localised would the whole group be found together.

GROUP SIZE, COMPOSITION, AND RANGE.

Methods of calculation.

If it is accepted that distinct groups exist, the next step is to determine their size, composition and home range. With open country primates repeated counts over a period of days are fairly consistent, and an accurate picture of group size and composition can readily be established. In the case of the blue monkey less direct methods have to be used; group

compositions must be calculated from a combination of counts of parties containing recognizable individuals. Suppose, for example, that a particular recognisable animal had been seen on one occasion with a male, two females, and a juvenile, and on another with three females and two infants. One could conclude that the group contained at least one male, three females, a juvenile, and two infants, besides the recognizable individual. From repeated sightings a complete picture of group composition can be built up.

For such an approach to be valid it must be assumed that the groups are closed social units; any interchange of individuals between groups would weaken its reliability. Movement of animals from one group to another has been recorded in other species (e.g: C.aethiops, Gartlan 1966, Presbytis entellus, Sugiyama 1967, Papio anubis, DeVore and Hall 1965, Rowell 1969), but such changes are generally few in relation to the overall stability of the group, and typically involve only adult males. While movement of individuals between groups would be difficult to detect in the blue monkey, it seems unlikely to be extensive.

Counts of parties vary in their reliability. Confusion is particularly likely to occur between the juvenile and infant categories. For instance a party

that appeared to contain three juveniles and two infants one day and two juveniles and three infants the next might come from a group containing three of each class, or alternatively from one with a total of five in the two classes combined, one animal being on the borderline between the two categories. Only the most reliable party counts have been used in the deduction of group composition.

Reconstruction of group composition from individual party counts may in some cases give only the minimum number of animals in each class, rather than the actual total. For the full number to be recorded all the individuals in a class must be seen together in the same party on at least one occasion. The extent to which underestimation occurs will depend on the size of the group and its degree of fragmentation. If groups are small and the whole group is sometimes found together the chances of distortion will be slight.

Another possible complication is that individuals from more than one group may in a few instances have been recorded as members of the same party. When there is reason to believe that this is the case such parties have been excluded from consideration.

Despite these difficulties, calculations of

group composition are not quite so haphazard as might at first appear. Although only a few monkeys were clearly recognisable beyond all doubt, many others were sufficiently distinctive to appear familiar when seen on succeeding days in the same place or in the company of more readily distinguishable animals. The characters by which these individuals could be recognised, such as nipple size and colour or bushiness of the tail, were not sufficiently constant or unique to set them apart from all other monkeys anywhere in the study area, but once the existence of distinct groups had been established they enabled the observer to build up a much more accurate picture of group composition than would otherwise have been possible.

Size and composition.

The approximate compositions of six groups were determined. Fig 2.9 (a) shows the compositions as at September 1966, soon after the existence of distinct groups had been established. Group D was known to be incompletely counted at this time. Fig. 2.9 (b) gives the compositions of groups A - D at the end of the study; groups E and F were not seen sufficiently often during the last few months for their compositions to be determined again.

It will be seen that there are slight differences between the two counts. The change in the composition of group A can be attributed to the known disappearance of one baby, growth of the remaining baby into an infant, and of one infant into a juvenile. The increase of two in the size of group B is in part accounted for by the birth of another baby. One juvenile would have grown to adult size. The baby recorded in group C in the first count would have grown to infant size by the end of the study; two more babies were born in the intervening period. Monkeys appear to have been lost from the juvenile/infant classes without any corresponding recruitment to the adult categories, but this may be the result of errors in the estimation of group composition rather than of emigration or death. Differences in the number of young animals in the two counts for group D are accounted for by the birth of another baby, growth of the original baby into an infant, and of one infant into a juvenile. The addition of two further adults can be ascribed to the earlier count being incomplete.

Both counts of group B include an adult female that appeared to be a hybrid between a blue monkey and a redtail, and an infant belonging to this female

FIG. 2.9 Group compositions.

(a). September I966.

Group	mature male	young male	female	unsexed adult	TOTAL ADULTS	juvs.	infant	baby	TOTAL
A	2	I	6	-	9	2	3	2	I6
B	I	-	3	2	6	3	3	-	I2
C	I	I	5	2	9	3	4	I	I7
D	I	I	3	-	5	I	3	I	I0(+)
E	I	I	4	-	6	2	4	-	I2
F	I	-	4	2	7	2	4	-	I3

(b). March I967

A	2	I	6	-	9	3	3	-	I5
B	I	-	4	3	8	2	3	I	I4
C	I	I	5	I	8	2	3	2	I5
D	I	I	4	I	7	2	3	I	I3

FIG.2.IO(a). The hybrid.

Fig.2.IO(b). The hybrid's infant.

(see fig. 2.10). These animals have been described in detail elsewhere (Aldrich-Blake 1968). The female was intermediate in appearance between the two species. The infant, presumably the issue of a mating between the hybrid and a male blue monkey, could pass for a blue monkey were it not for a white spot on its nose, a characteristic of C.ascanius. Both the hybrid and its infant appeared to behave no differently from other members of the group.

Group size ranges from 12 to 17, with a mean of 13.3 for the six groups in the September count and 14.25 for the four groups in the March count. If the incomplete count for group D is omitted from the first set of compositions the mean size of the remaining five groups is 14.0. These figures fall within the range of group size observed for other arboreal monkeys. (See Chapter 9 for a detailed comparison).

With one exception, each group contained only one mature male. Group A had two mature males, one of which was noticeably larger than the other. The mature male to female ratios for the two counts are 1:3.6 and 1:3.8; if known young adult males are included there are still more than twice as many females as males. In actual fact the discrepancy may be less than this since unsexed adults are more likely to be young adult

babies) ratios are 1:1.5 and 1:1.3 for the two counts. Since some unsexed adults will be females the true ratios must be slightly lower. Since the monkeys are classified as adults from three years of age, the maximum theoretical ratio, assuming that all females had a baby each year and no animals died before attaining adulthood, would be rather less than 1:3.0. At least 16 babies are known to have been born in groups A-D during or immediately before the study, giving a rate of about 9 births a year for the 19+ females in these groups. If this rate were maintained over a three year period one would expect the four groups to contain about 27 immatures; in fact they contain 25-26. Hence the difference between theoretical and observed female/immature ratios is probably the result largely of perinatal mortality or failure of females to conceive as often as once a year, rather than of mortality among infants and juveniles. (The significance of male/female and female/young ratios is discussed further in Chapter 9).

Home range.

With open country species a troop can generally be followed throughout the day, and a picture of the range built up by plotting daily movements over several days. In the case of the blue monkey the

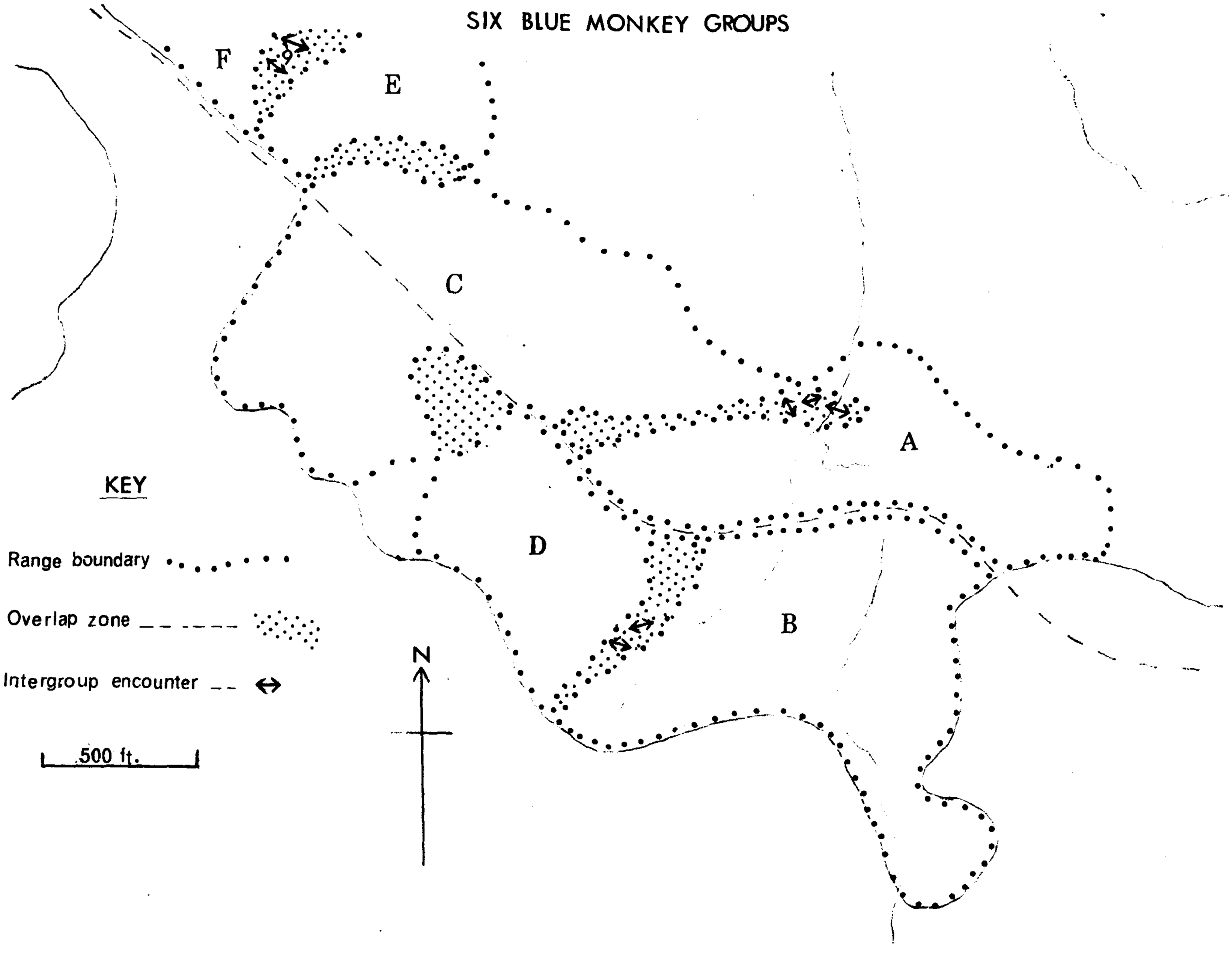
fragmentation of the group and the difficulties of maintaining contact with the animals for long periods renders this approach impracticable, particularly since it was not always clear to which group the party of monkeys being watched belonged. Home ranges have therefore to be deduced from sightings and movements of the recognizable individuals in each group and other monkeys seen associating with them.

Ranges of the six groups, calculated in this way, are shown in fig. 2.11. Also plotted are the locations of supposed intergroup encounters as described above (p.86). It will be seen that these fall in every case within the overlap zone between ranges. Since some of these incidents did not involve any recognisable individuals, they could in theory fall anywhere within the study area. The fact that they do not provides a measure of independent confirmation of the validity of the method of deducing range boundaries.

The northern boundary of group A's range is uncertain, but the range probably does not extend much deeper into the forest than is shown. Other groups of blue monkeys lived in the region to the north and east of groups A and C's ranges, but could not be identified with any certainty. The extents of groups E and F's

FIG.2.11 HOME RANGES OF

SIX BLUE MONKEY GROUPS



ranges are imperfectly known.

Groups A, B, and D's ranges are bounded on one side by the road that runs through the study area. Group C's range straddles the road. The canopy over the road is more continuous over its western end, in group C's range (see figs. 1.11, 1.12, and 1.13), but there are several places in the eastern half where monkeys could cross it without descending to the ground. Redtails and colobus monkeys sometimes crossed the road in this region, but blue monkeys were never seen to do so. Although the road does not form a complete barrier to movement, it appears to define the boundary of these groups' ranges. The forest edge provides another natural boundary to home ranges. Elsewhere boundaries do not follow any natural features.

The areas of the home ranges are: group A, at least 0.025 sq. miles, group B, 0.035 sq. miles, group C, 0.045 sq. miles, and group D, 0.020 sq. miles (mean 0.031 sq. miles). Much of group C's range is young forest with many open spaces, which reduces the effective area available to the monkeys; this may account for its greater size.

Considering the method used to map them the areas may be slight underestimates, and the overlap zones between ranges may be larger. Either group C or D,

or both, used the small blank area of forest on the southern edge of the study area. Group D's range may extend about 100 yards north of the road into group C's area; a recognisable individual from group D may have been seen there on one occasion, but identification was uncertain. Allowing for the overlap between ranges, the population density is about 475 sq. mile. Range size and population density in other arboreal monkeys are comparable (see Chapter 9).

DISCUSSION.

It is instructive to consider the contrast between the final picture of blue monkey population structure and the impression that would be gained from superficial study. A casual observer walking through the forest at a time when feeding conditions were typical would seldom see more than five or six monkeys together, and any notions of group size and composition based on such sightings would most likely be totally erroneous. Yet it is not unknown for 'group counts' of forest monkeys based on a single sighting to reach the literature, and while the authors themselves may be aware of the shortcomings of such counts, there is a risk that they may be accorded too great a weight in subsequent citations. The results of a casual encounter become elevated to the 'mean group size'

for a species, and may be used in comparison with data on other species much of which will rest on a more secure foundation. This is not to say that data derived from small numbers of sightings are entirely without value, but the dangers should be appreciated. If, for instance, a visitor to Budongo happened to hit on a time when fig trees or some other prolific species were fruiting, his impressions of blue monkey grouping tendencies would be entirely different to those of our casual observer above. Even if an observer spent several weeks in intensive study he still might not establish the basic pattern of social organisation unless he was lucky enough to see clear cut territorial encounters; indeed after six months of my own study I was almost convinced that blue monkeys had no distinct group structure, but rather a pattern of organisation similar to the chimpanzee. Only after nine months was it clear that this view was erroneous. Admittedly the true pattern is most likely to be obscured in species such as the blue monkey and the redtail, in which groups are not compact and well-defined, but even in species that do live in compact groups data may be distorted. The moral to be drawn is clear. A reliable picture of the social organisation of a forest species can be obtained only by prolonged study; the results

of casual observation or short term projects can be positively misleading.

Chapter 3

DAILY ACTIVITIES AND USE OF HABITAT

DIURNAL ACTIVITY CYCLE.

Blue monkeys generally become active soon after sunrise, though the time at which they leave their sleeping positions varies considerably from day to day. As a rule the first activity is an intensive bout of feeding lasting 1 - 1½ hours, but this may be preceded by a period of grooming, playing, or just sitting in the sun. During the dry season the frequency of feeding decreases rapidly in mid-morning. Activity may cease as early as 0900 hrs and all the monkeys move into thick creepers or foliage, whence they may not emerge again until 1 - 1½ hours before sunset. There is then a further bout of intensive feeding in the hour before dark. During the rainy season the activity cycle is more variable. The intensity of feeding falls off more gradually in the morning and there may be further bouts of feeding in the late morning or early afternoon. If the monkeys do become inactive in the middle of the day they resume activity much earlier than in the dry season, often by 1430 or 1500 hrs. In both seasons the animals take up their sleeping positions in the 20 to 30 minutes between sunset and darkness.

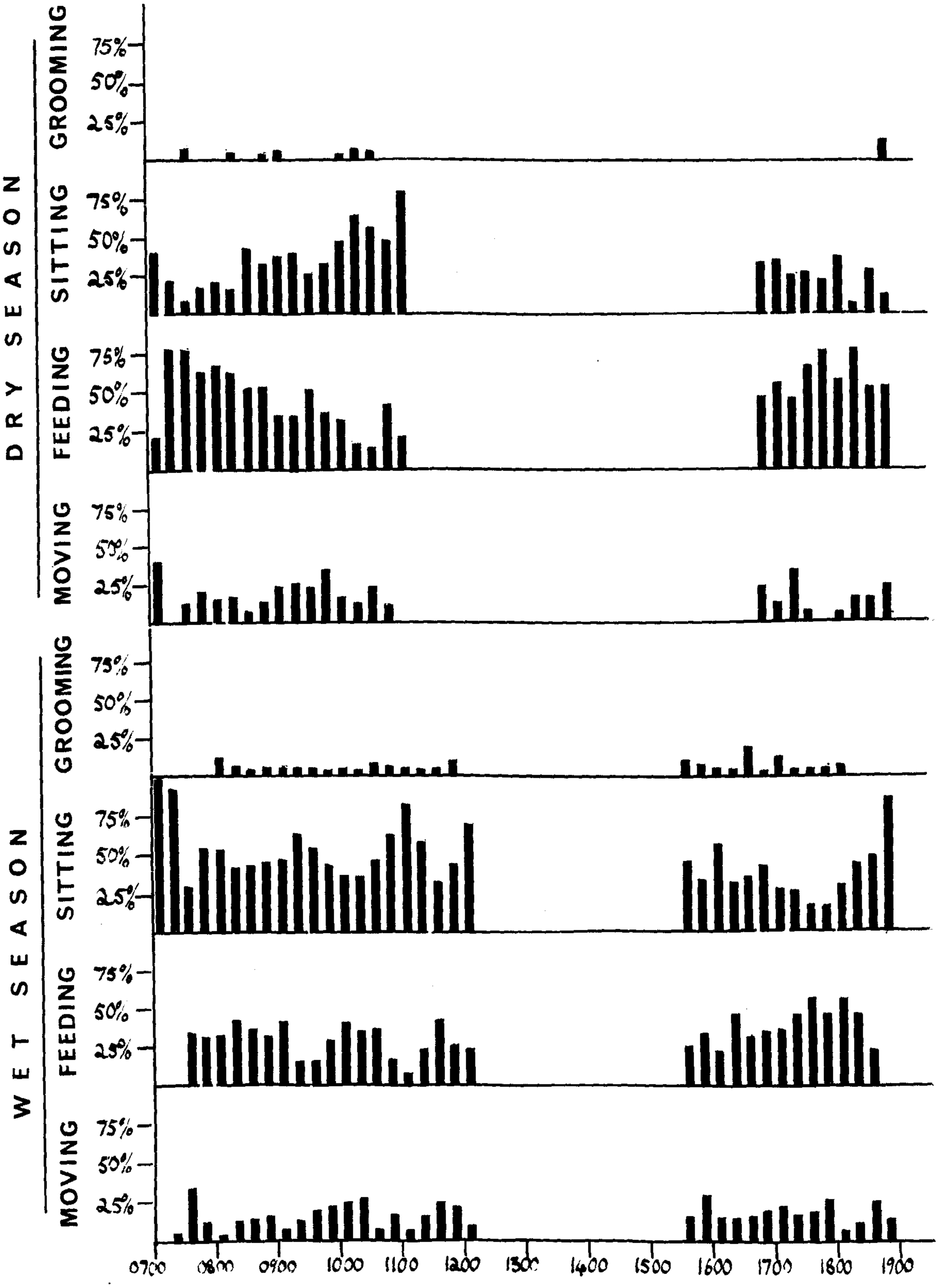
Quantitative confirmation of these patterns of activity was obtained in the following way. At 15

minute intervals a count was made of all monkeys visible at that particular moment, and their activity recorded. Four categories of activity, grooming, sitting, feeding, and moving, were recognised; other activities such as play or copulation were too infrequent to merit quantification. The results obtained are expressed in fig. 3.1. The day is divided up into 15 minute periods. Counts of each activity for each 15 minute period are summed and expressed as a percentage of the total number of monkeys seen in counts during that period. Data for the middle of the day are omitted, there being insufficient counts at that time to give an accurate picture. Data for the wet and dry seasons are given separately.

Fig. 3.1 shows clearly that during the dry season feeding is confined to the early morning and late evening. During the rainy season, on the other hand, it is spread more evenly throughout the day, though there is still a peak in the evening and to a lesser extent in the morning as well.

These seasonal differences in diurnal activity are probably related primarily to climatic factors, particularly temperature. During the dry season days are almost invariably cloudless, and maximum shade

FIG. 31 RELATIVE FREQUENCIES OF VARIOUS ACTIVITIES AT DIFFERENT TIMES OF DAY



temperatures are around 90°F. The temperature in the direct rays of the sun would be very much higher. It is already very hot by 0900 hrs, and does not begin to cool down appreciably until 1600 or 1700 hours. In the rainy season the weather is more variable. It may be overcast at dawn, but the morning is usually sunny. Cloud begins to build up from mid-morning on, culminating in thundery rain any time after mid-day. It may clear again in the evening, or rain may continue until dusk. Maximum shade temperatures are lower, between 75°F and 85°F, and the daily march of temperature is less regular. As much of the day is cloudy the monkeys are less often exposed to direct sunlight. While detailed records linking temperature and activity are lacking ... shade temperatures near the forest floor would anyway be unrepresentative of the microclimate experienced by the monkeys ... qualitative observations suggest that the animals are indeed sensitive to minor changes in temperature. Monkeys that were active during cloudy periods in the middle of the day often became inactive as soon as the sun came out, and resumed activity when it went in again.

The level of activity is influenced also by rain. During light rain the monkeys carried on with whatever

they were doing, but in heavier showers they moved into thick foliage and sat with shoulders hunched and head low until the rain stopped.

To give a typical example, on the evening of 27/10/66 I was watching a party of six monkeys, three adults, a juvenile and two infants, feeding. At 1755 hrs it began to rain heavily. All but two of the monkeys at once disappeared into thick foliage. One adult moved under a thick clump of leaves, carrying a seed pod with it, and continued eating. A second adult stopped feeding and shook itself, but remained sitting, in the open, with shoulders hunched. After 5 minutes this adult jumped down into thick bushes and disappeared, and a couple of minutes later the second adult moved into thicker foliage also. By 1810 the rain was slacking off; the juvenile moved up onto a bare branch and sat scratching itself and looking around, and an infant emerged and started moving about. At 1815 the rain stopped. The juvenile and infant resumed feeding, and an adult reappeared and started feeding also. By 1820 the whole party were feeding again.

Many showers last no longer than 20 to 30 minutes. If, however, rainfall is prolonged, the monkeys may become active again before it ceases. Moreover rain in the early morning, when the monkeys have not fed for 12 hours, is less likely to prevent activity than rain later in the day. For instance, on 28/10/66 there was torrential rain from before dawn until 1030 hrs. Monkeys were active by 0745, and fed intensively for three quarters of an hour despite the rain.

A similar cycle of behaviour to that shown by the blue monkey in the dry season, active morning and evening and inactive during the middle of the day, has

been recorded in many other primates (e.g: C.ascanius, Haddow 1952, Erythrocebus patas, Hall 1965, Macaca mulatta, Southwick et al 1965), and indeed in other tropical animals also (e.g: barasingha, Cervus duvauceli, blackbuck, Antilope cervicapra, Schaller 1967). Chivers (1969) noted a comparable transition from peaks of activity in morning and evening to a less regular pattern during the rains in Alouatta palliata. On the other hand the mangabeys studied by Chalmers (1967, 1968a) in forests on the northern shores of Lake Victoria, where climatic conditions fluctuate but little during the year, showed three peaks of activity, one in morning and evening and one in the middle of the day as well. A state of affairs comparable to that in blue monkeys and howlers was found by Bell and Aldrich-Blake (unpublished data) in the wildebeeste, Chonochaetes taurinus albojubatus. Wildebeeste in the hot, low-lying western corridor of the Serengeti confined their grazing to the early morning and late evening, whereas those in the higher and cooler Ngorongoro crater were active throughout the day.

USE OF CANOPY LAYERS.

While it has often been stated that forest

monkeys confine their activities to a particular level in the canopy (e.g: Booth 1957, Napier 1962), this assertion is seldom supported by quantitative evidence. Indeed only Chalmers (1967, 1968a) appears to have collected quantitative data of this kind; he was able to show that Cercocebus albigena spends proportionally more of its time in the available canopy above 70 ft. than below this height.

In the present study, at each 15 minute activity count the canopy layer that each monkey was in was recorded. For these purposes the canopy was divided into three layers. The lower layer was taken to extend from ground level up to 35 ft, the middle canopy from 35 ft. to 70 ft, and the upper canopy from 70 ft. upwards. These divisions correspond broadly to the main vegetational layers in the various forest types. Hence figures are available both for the number of sightings in each layer and for the relative frequency of individual activities in the three layers. Differences in the ease of observing monkeys in the various layers are considered insufficient to invalidate quantitative comparisons. These data are shown in fig. 3.2 The wet and dry seasons are again treated separately. In figs. 3.3 and 3.4 the same data are expressed as percentages, firstly for each activity

FIG.3.2 Frequencies of various activities in the different canopy layers.

(a). Dry season.

	Ground	Lower canopy	Middle canopy	Upper canopy	TOTAL
Grooming	-	4	I8	-	22
Sitting	-	97	247	83	427
Feeding	-	I34	288	233	655
Moving	I	44	I28	40	2I3
TOTAL	I	279	68I	356	I3I7

(b). Wet season.

Grooming	-	2	24	I8	44
Sitting	I	87	34I	205	634
Feeding	-	75	256	I37	468
Moving	2	I7	I77	37	233
TOTAL	3	I8I	798	397	I379

FIG.3.3 Frequencies of activities in the different canopy layers, as percentages, treating each activity separately.

(a). Dry season.

	Ground	Lower canopy	Middle canopy	Upper canopy	TOTAL
Grooming	-	I8.I	8I.9	-	I00
Sitting	-	22.8	57.8	I9.4	I00
Feeding	-	20.5	44.0	35.5	I00
Moving	0.5	20.6	60.I	I8.8	I00
ALL ACTIVITIES COMBINED	-	2I.3	5I.7	27.0	I00

(b). Wet season.

Grooming	-	4.5	5445	4I.0	I00
Sitting	0.2	I3.7	53.8	32.3	I00
Feeding	-	I6.0	54.7	29.3	I00
Moving	0.8	7.3	76.0	I5.9	I00
ALL ACTIVITIES COMBINED	0.2	I3.I	57.9	28.7	I00

FIG.3.4 Frequencies of activities in the different canopy layers, as percentages, treating each layer separately.

(a). Dry season.

	Ground	Lower canopy	Middle canopy	Upper canopy	ALL LAYERS COMBINED
Grooming	-	I.4	2.6	-	I.7
Sitting	-	34.8	36.3	23.3	32.4
Feeding	-	48.0	42.3	65.5	49.7
Moving	I00.0	I5.8	I8.8	II.2	I6.2
TOTAL	I00	I00	I00	I00	I00

(b). Wet season.

Grooming	-	I.I	3.0	4.5	3.2
Sitting	33.7	48.I	42.7	5I.6	46.0
Feeding	-	4I.4	32.I	34.5	33.9
Moving	66.7	9.4	22.2	9.3	I6.9
TOTAL	I00	I00	I00	I00	I00

separately and secondly for each layer separately.

In both wet and dry seasons the number of records in each layer differs from that which would be expected were all layers used equally (X^2 = 422.9 and 206.7 respectively, with two degrees of freedom. p = <0.001 in each case). The middle canopy accounts for half or more of the total, with the remainder being divided unevenly between the upper and lower canopies. Of 2636 individual records, only 4 are of monkeys on the ground. These are included in the lower canopy scores for purposes of analysis.

The distribution of activity as a whole between the various layers differs significantly between wet and dry seasons (X^2 comparihg column totals in figs. 3.2 (a) and (b) is 29.94 with 2 d.f. p = <0.001). The proportion of monkeys in the upper canopy is similar, but in the dry season more of the remaining sightings are in the lower canopy than in the wet season, 21% as against 13%.

If records of individual activities for the two seasons are compared, further differences are revealed. Thus the zonation of sitting differs significantly between seasons (X^2 = 27.82 with 2 d.f. p = <0.001); in the wet season 32% of all sitting records are in the upper canopy, as opposed to only 19% of the dry season, when there is more sitting in the lower canopy.

Likewise the zonation of feeding differs also (X^2 = 12.66 with 2 d.f. p = <0.01); during the rains more than half of all feeding takes place in the middle canopy, whereas in the dry season it is spread more evenly over the three layers. Or to express it another way, in the dry season 23% of the records in the top canopy are for sitting and 66% for feeding, whereas in the wet season 52% are for sitting and 35% for feeding. (X^2 comparing upper canopy records for the two seasons is 92,75 with 3 d.f. p = <0.001). In other words although the distribution of food apparently compels the monkeys to do much of their feeding in the upper canopy during the dry season, when inactive they spend proportionally more of their time lower in the canopy than in the wet season.

This can readily be explained by the difference in climate between the two seasons. In the dry season, when it is hot and sunny all day and some trees are leafless, there is little shade in the upper layers of the canopy. Obviously the lower down in the canopy a monkey goes, the deeper will be the shade that it can find. If the animals avoid extremes of temperature they will naturally tend to be found lower in the canopy. In the wet season this argument does not apply to the same extent, since the weather

is cooler and less sunny. It was noticeable that in the dry season monkeys that remained feeding in the upper canopy for more than an hour or so after sunrise tended to move into such little shade as they could find, whereas in the wet season they would often remain in the open at the top of the canopy.

(The use of the X^2 test in this context could be criticised on the grounds that repeated counts were made on the same animals; the data are hence not fully independent. This limits the conclusions that can be drawn; no statements can be made about the behaviour of an individual monkey, nor, strictly speaking, is it possible to generalise the findings of any wider population of monkeys. Only hypotheses relating specifically to those monkeys sampled, as a group, can be tested. (Lewis and Burke 1949, Siegel 1956).

Since, in the present case, sampling was randomly repetitive and the interval between counts was sufficient to allow monkeys to change their activity or move from one layer to another, the weight of these strictures would be lessened. Extensive use is made of the X^2 test in forthcoming chapters, and this difficulty should be born in mind for future reference.

DAILY RANGE AND PATTERN OF MOVEMENT.

Many primate field studies give maps showing the movements of groups on successive days. For various reasons this approach is inappropriate in the case of the blue monkey. The total spread of the group is large in relation to the distance travelled in a day and the size of the home range, and the group seldom

moves as a coordinated unit; monkeys from the same group often differ considerably in their daily movements. One can hardly ever see more than a few members of the group at the same time, and one can seldom retain contact with an individual or small party, let alone the entire group, for more than a few hours.

Daily movements are better illustrated by mapping the day ranges of recognisable individuals rather than whole groups, or by noting the location and direction of movement of all the monkeys in sight at frequent intervals during periods of observation. These methods give an idea both of the total distance travelled by a typical monkey in the course of a day, and of the degree to which members of the group are moving as a cohesive unit.

Fig. 3.5 shows the movements of a recognisable individual, the hybrid female in group B, during the week of Oct. 2nd - 8th, 1966. The greatest movement recorded in a day was 1000 yards; this is probably near the upper limit of daily range. A monkey moving as much as this in a day might cover much of its home range. The distance travelled in a day was often much less; if all the monkeys' feeding requirements were provided by a single tree they might move no more than 150 yards from it during the entire day. In the

present instance there were two main sources of food in the area, a fruiting Ficus natalensis and a scattered group of Funtumia spp. with a heavy crop of pods (see fig. 3.5). Most members of the group visited both of these at least once in the course of the day. The western part of the home range contained several Cynometra alexandri with young leaves and pods. In addition to providing a small amount of food these trees gave deeper shade than could be found in other parts of the range. They were frequently visited in the middle of the day.

During the week covered the hybrid's movements show some regularity from day to day, but such regularity would not be maintained over a longer period. It is due in part to the restricted location of food, and in part to the nature of the canopy in the vicinity of the feeding trees. In colonising forest there are many open spaces which break up the canopy; the monkeys avoid descending into the shrub layer to cross them and so tend to use the same trees in moving from one point to another. The fig tree was bordered on two sides by clearings made by fallen trees, so it could be approached by only a limited number of routes. In more mature forest, on the other hand, the canopy is continuous and the animals can move in a more or

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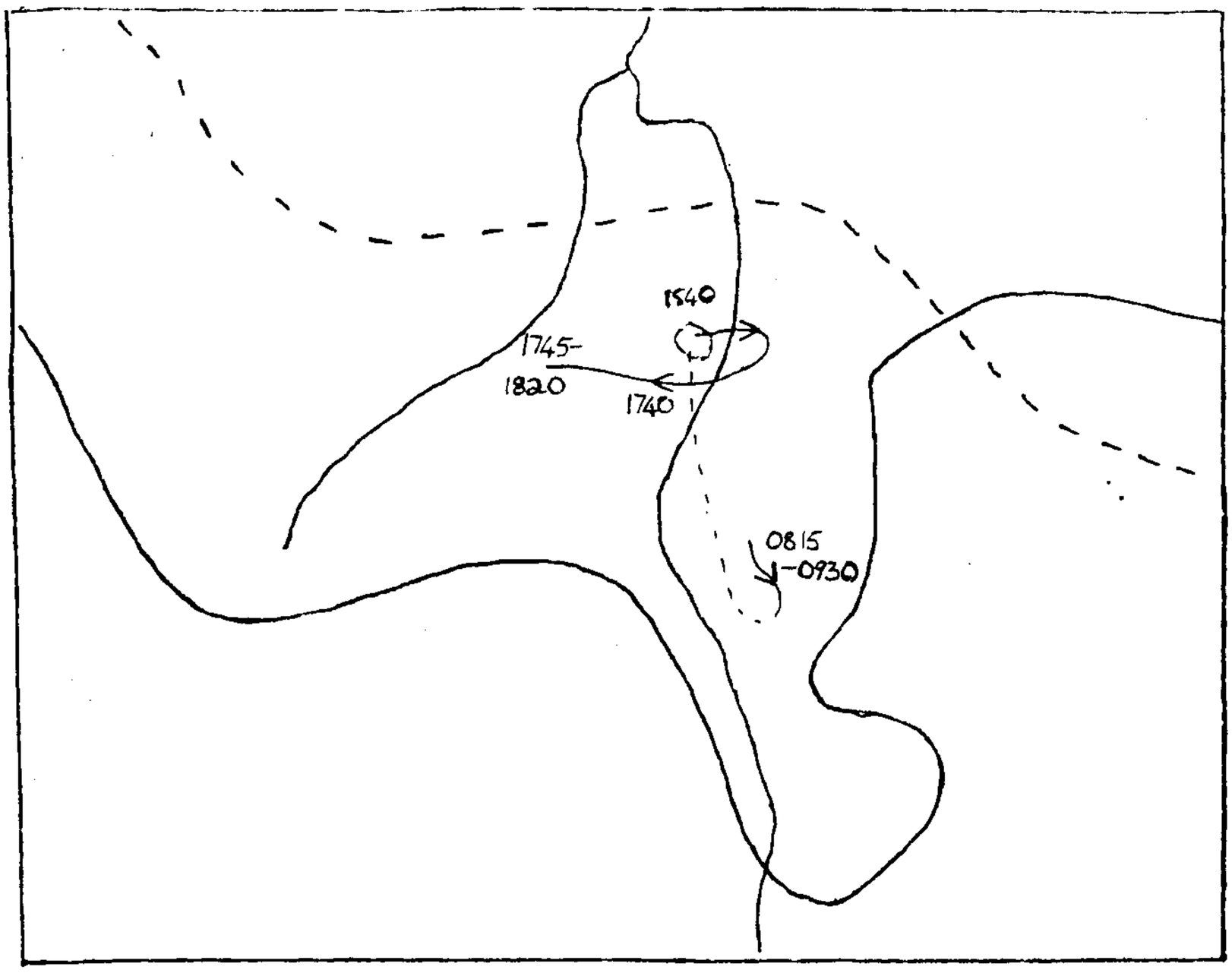
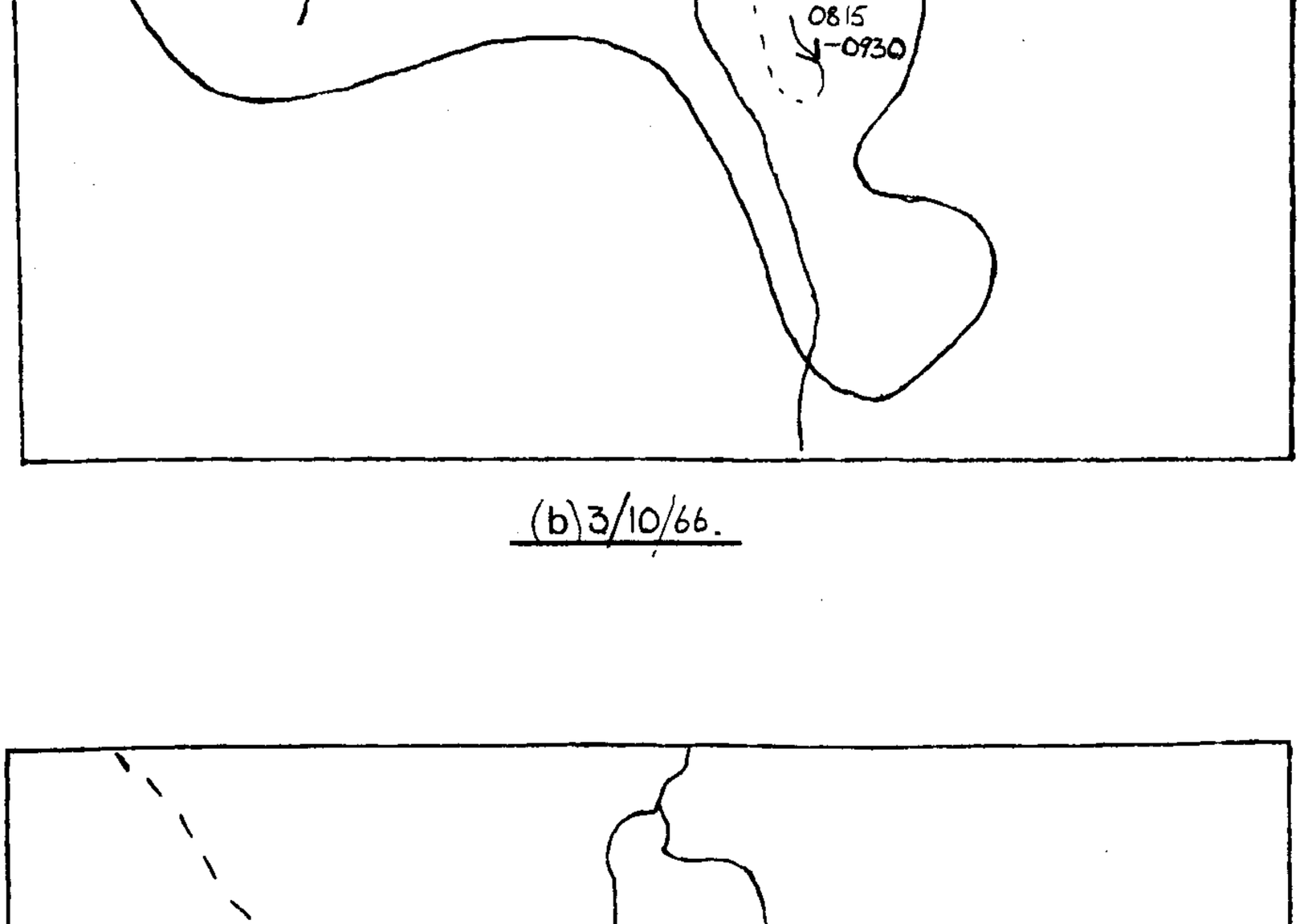
FIG. 3.5 (cont.)

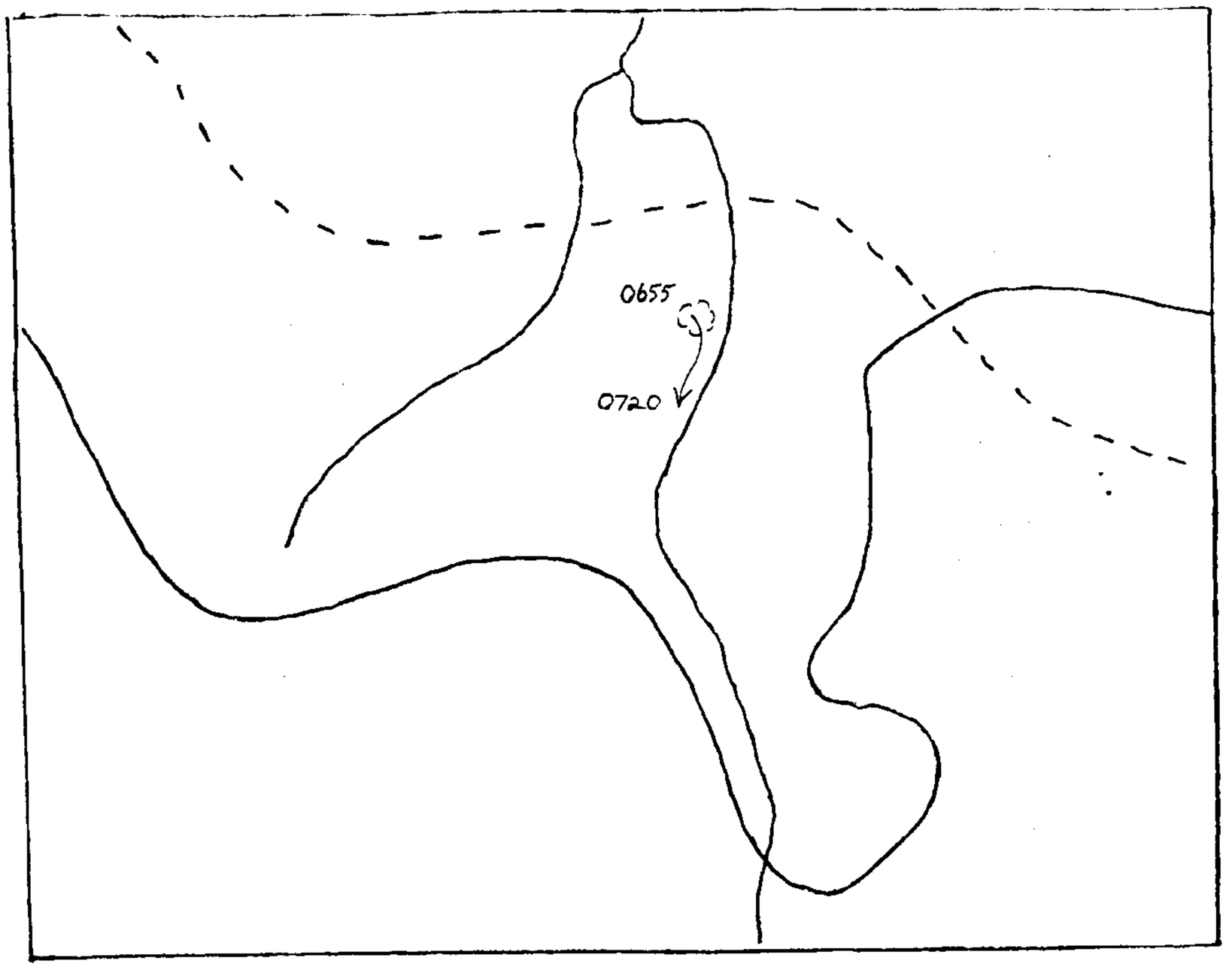


(b) 3/10/66.



(c) 4/10/66.

FIG. 3.5 (cont.)



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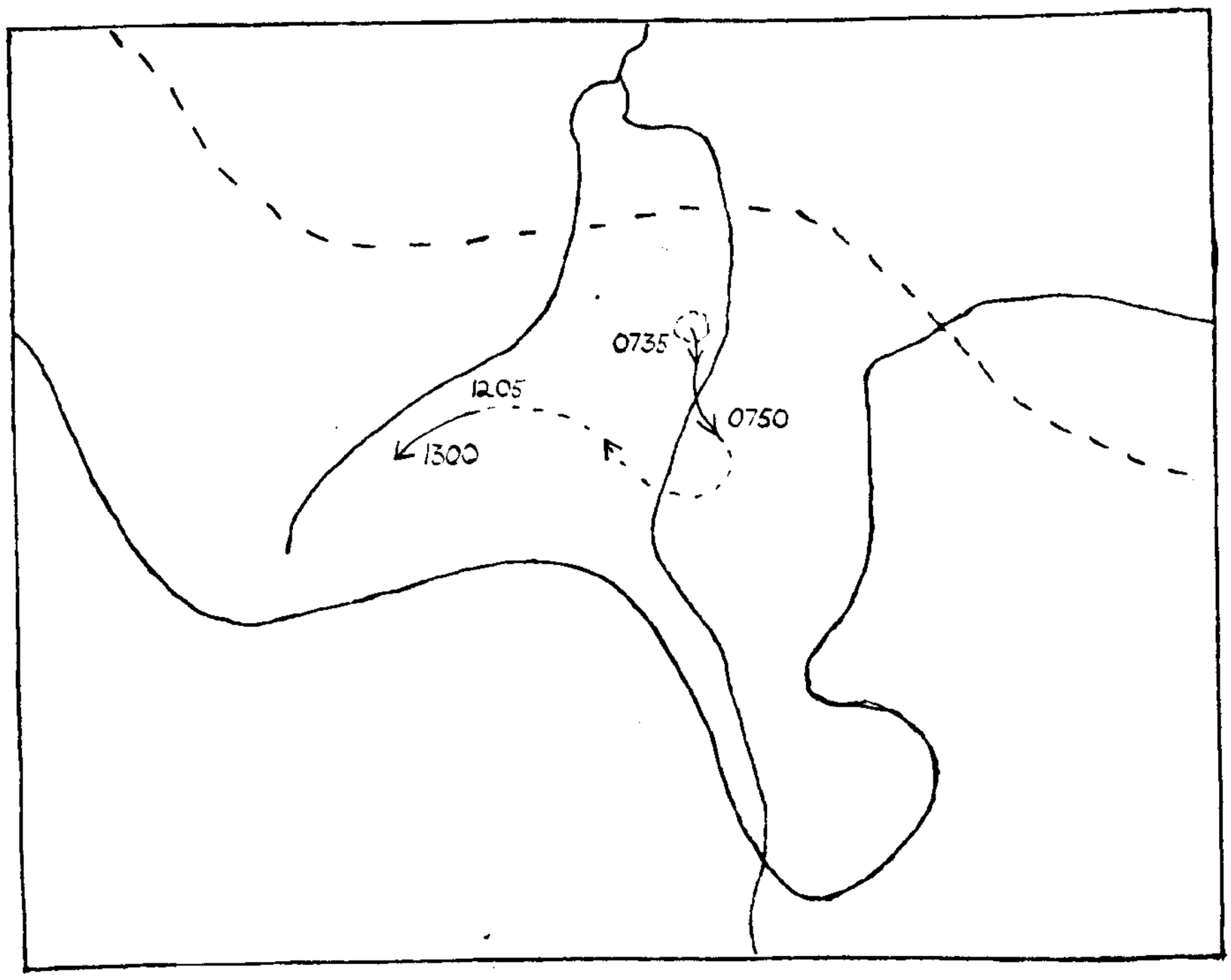

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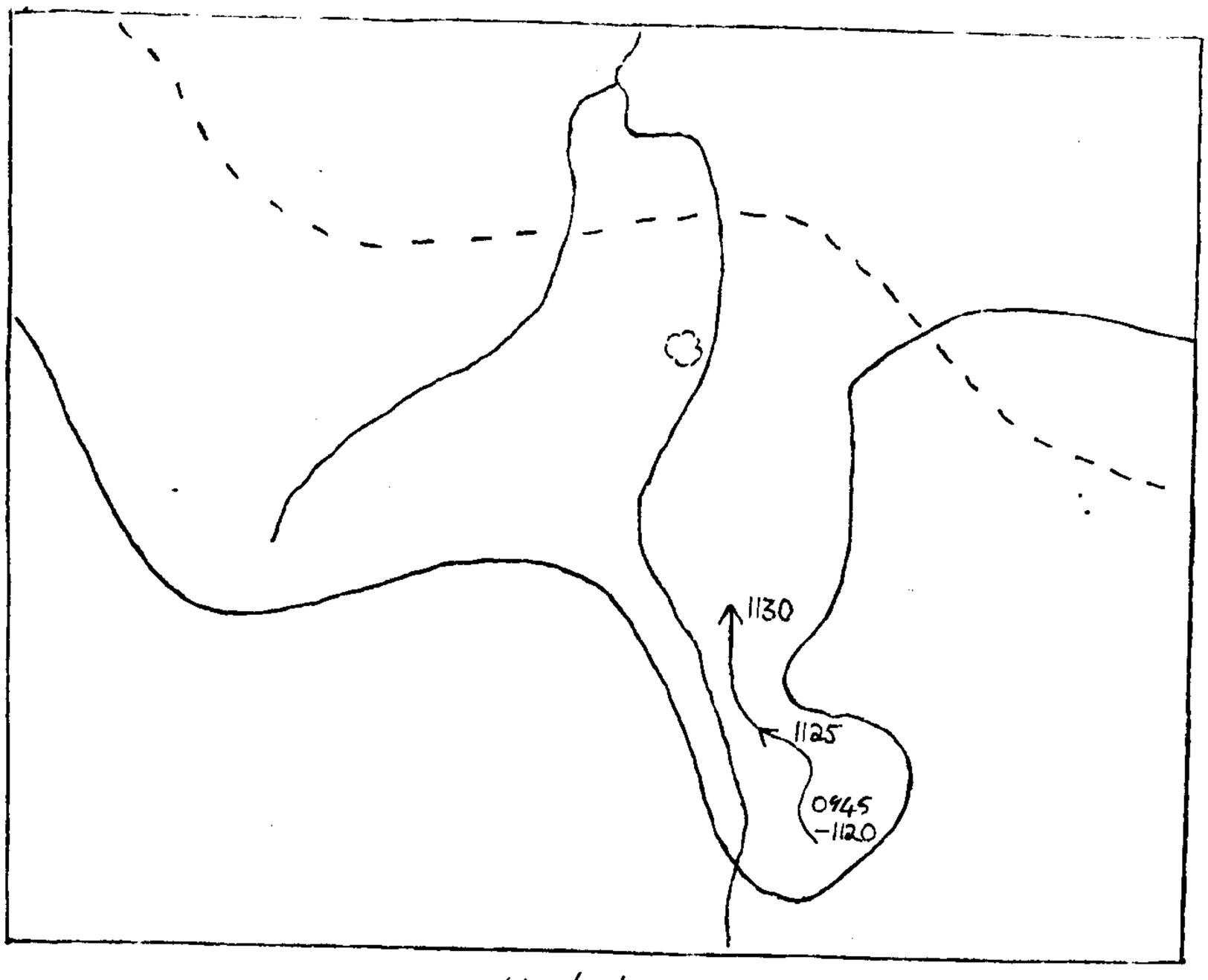
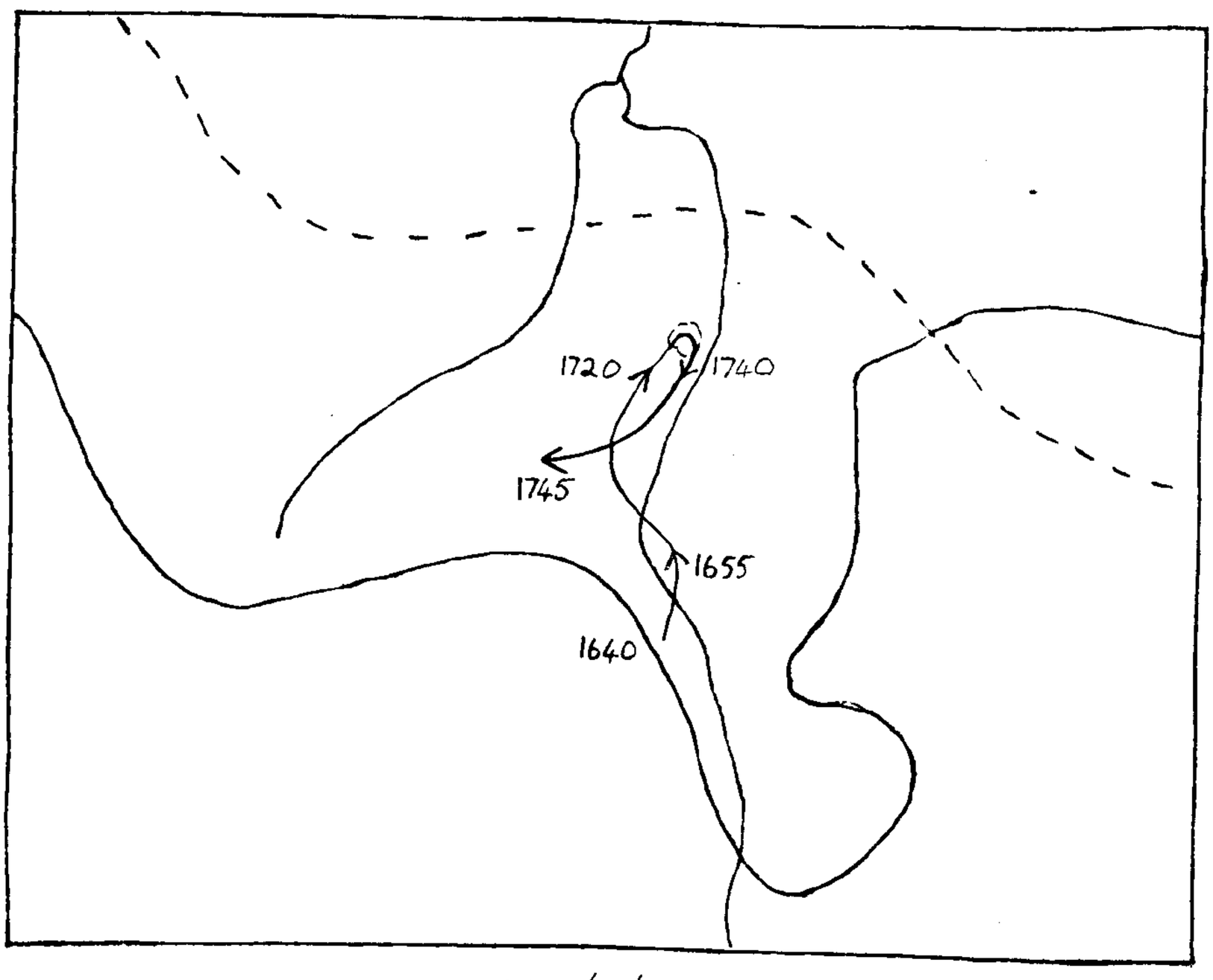
FIG. 3.5 (cont.)

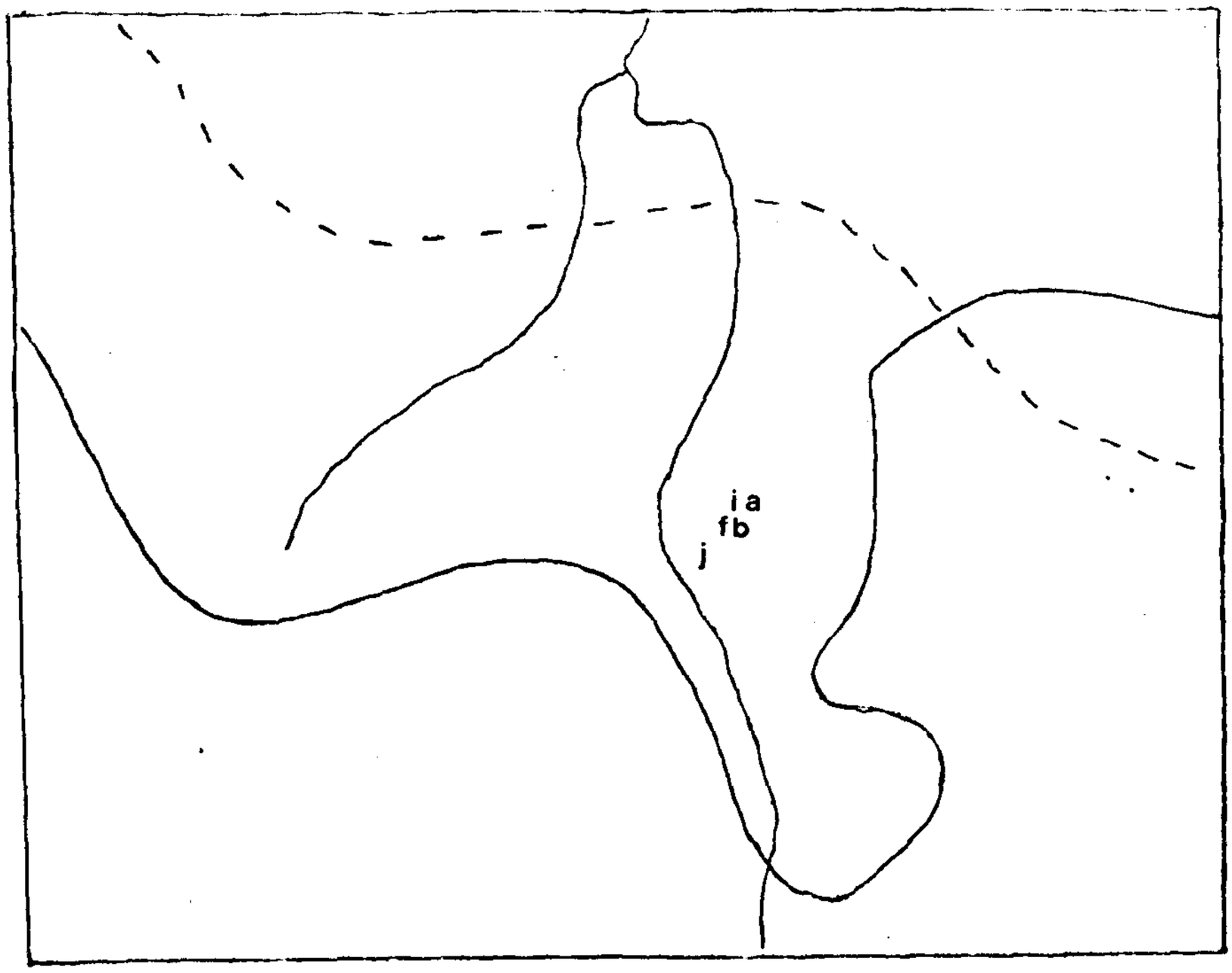


(f) 7/10/66.



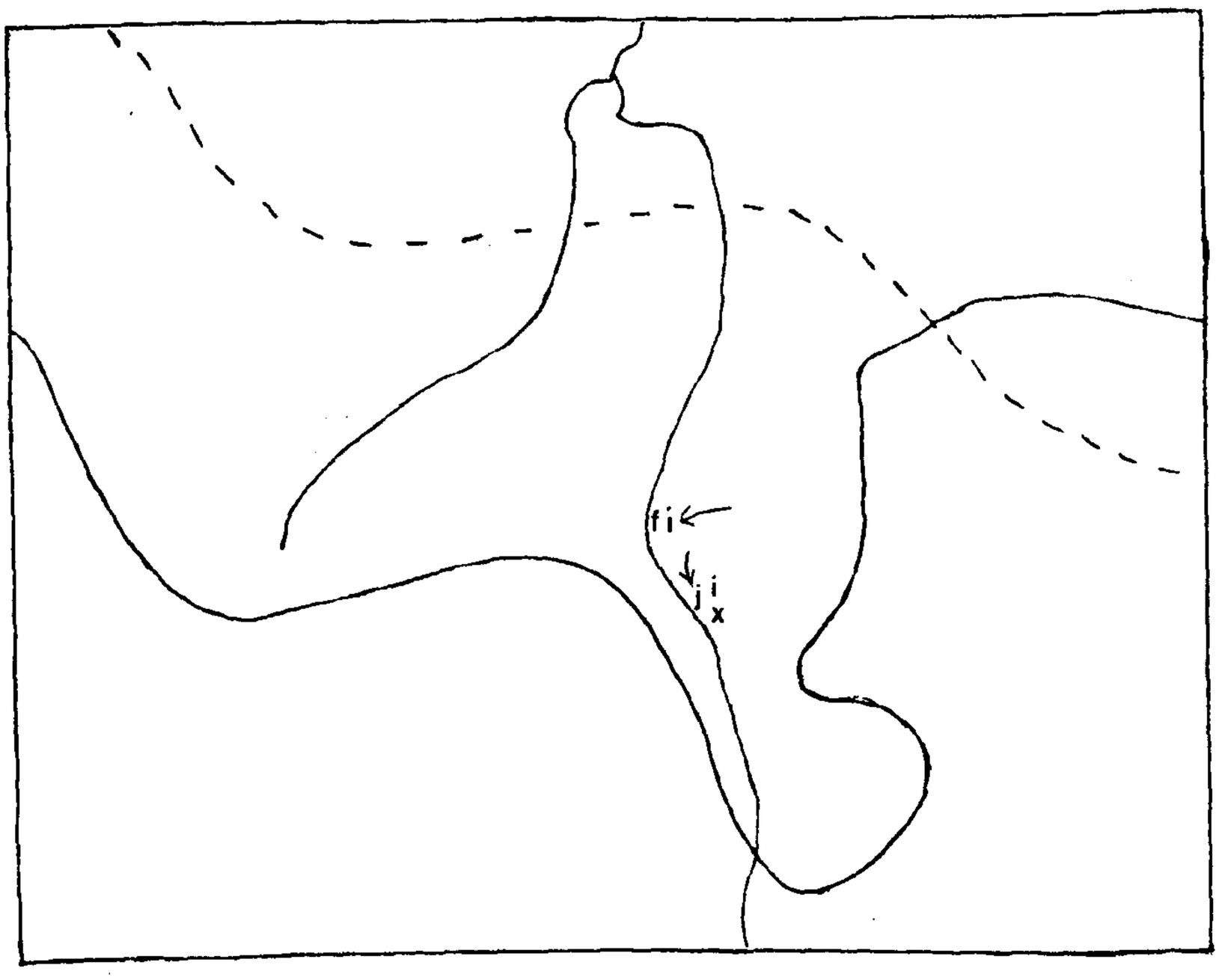
(g) 8/10/66.

FIG. 3.6 POSITIONS OF MONKEYS AT HALF-HOURLY INTERVALS



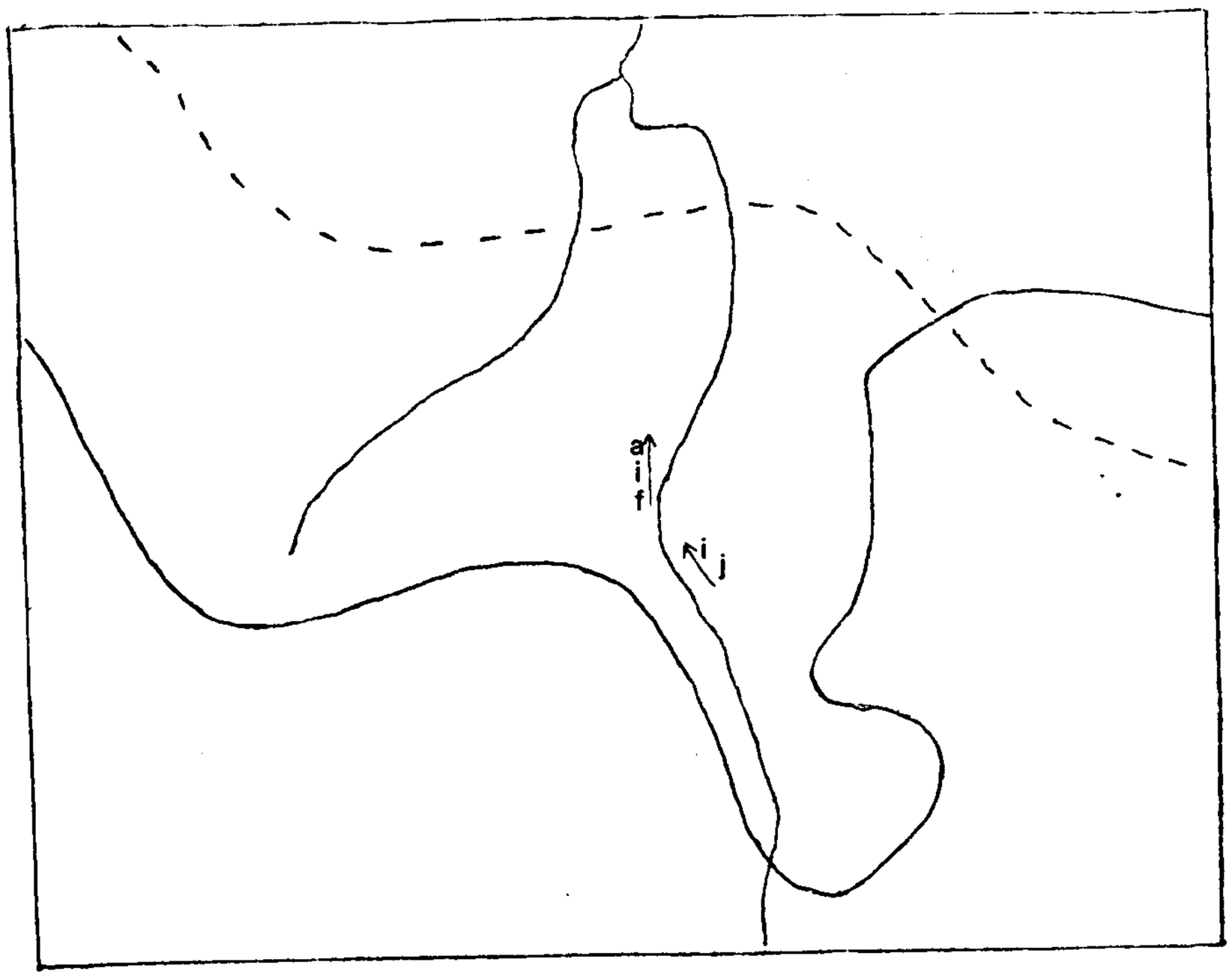
(a) 0900

m_male, f_female, a_unsexed adult, j_juvenile,
i_infant b_baby.

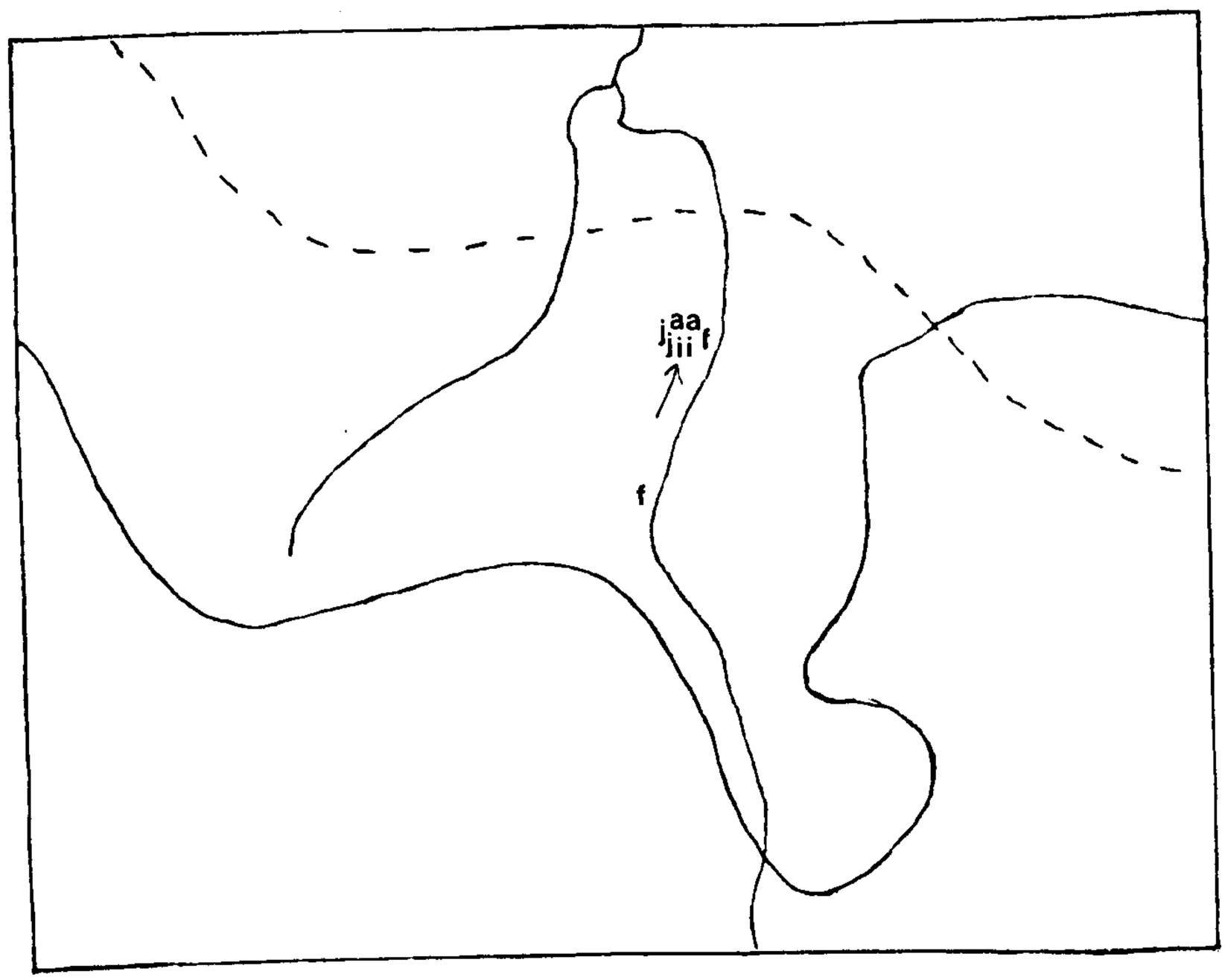


(b) 0930

FIG. 3.6 (cont.)

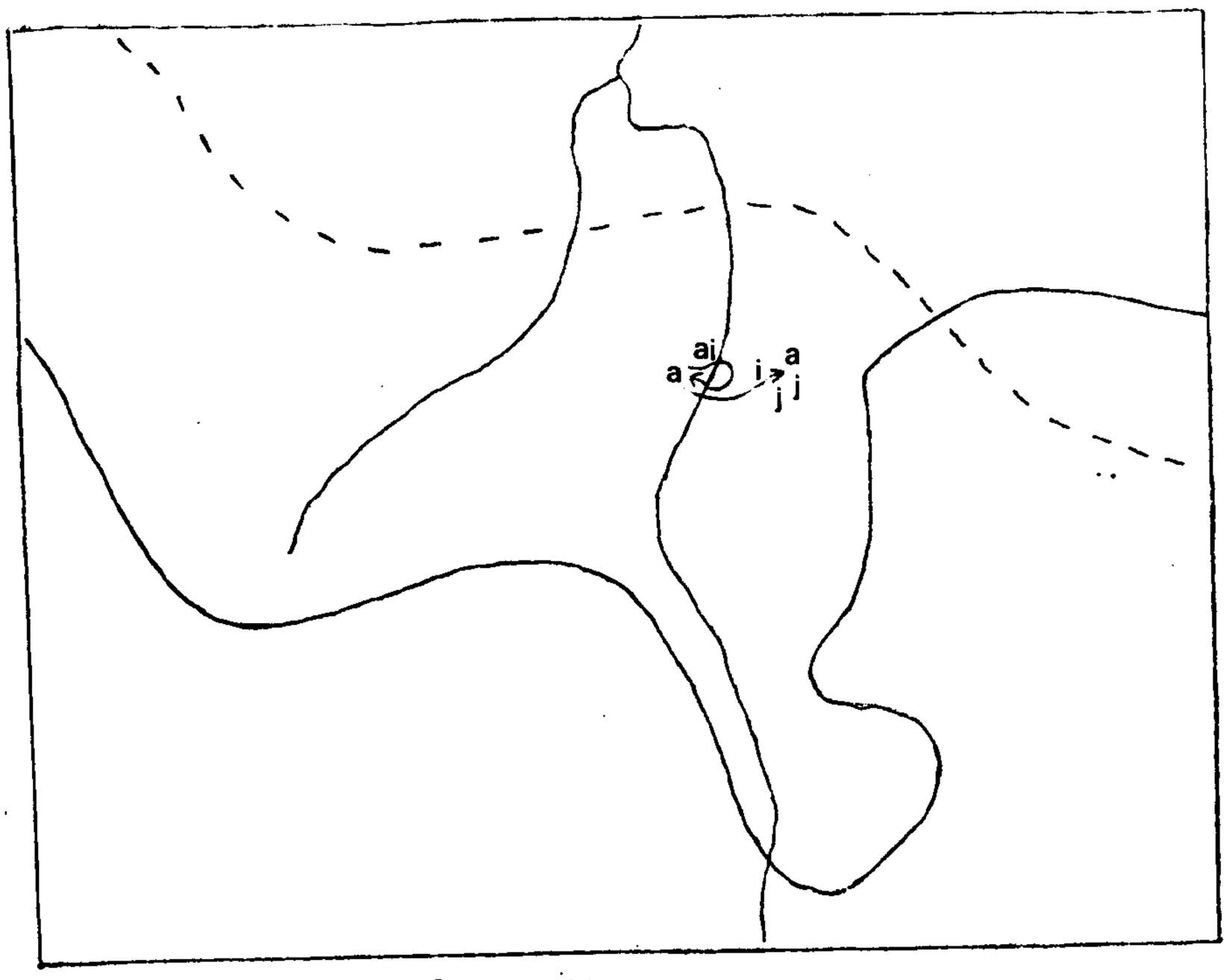


(c). 1000

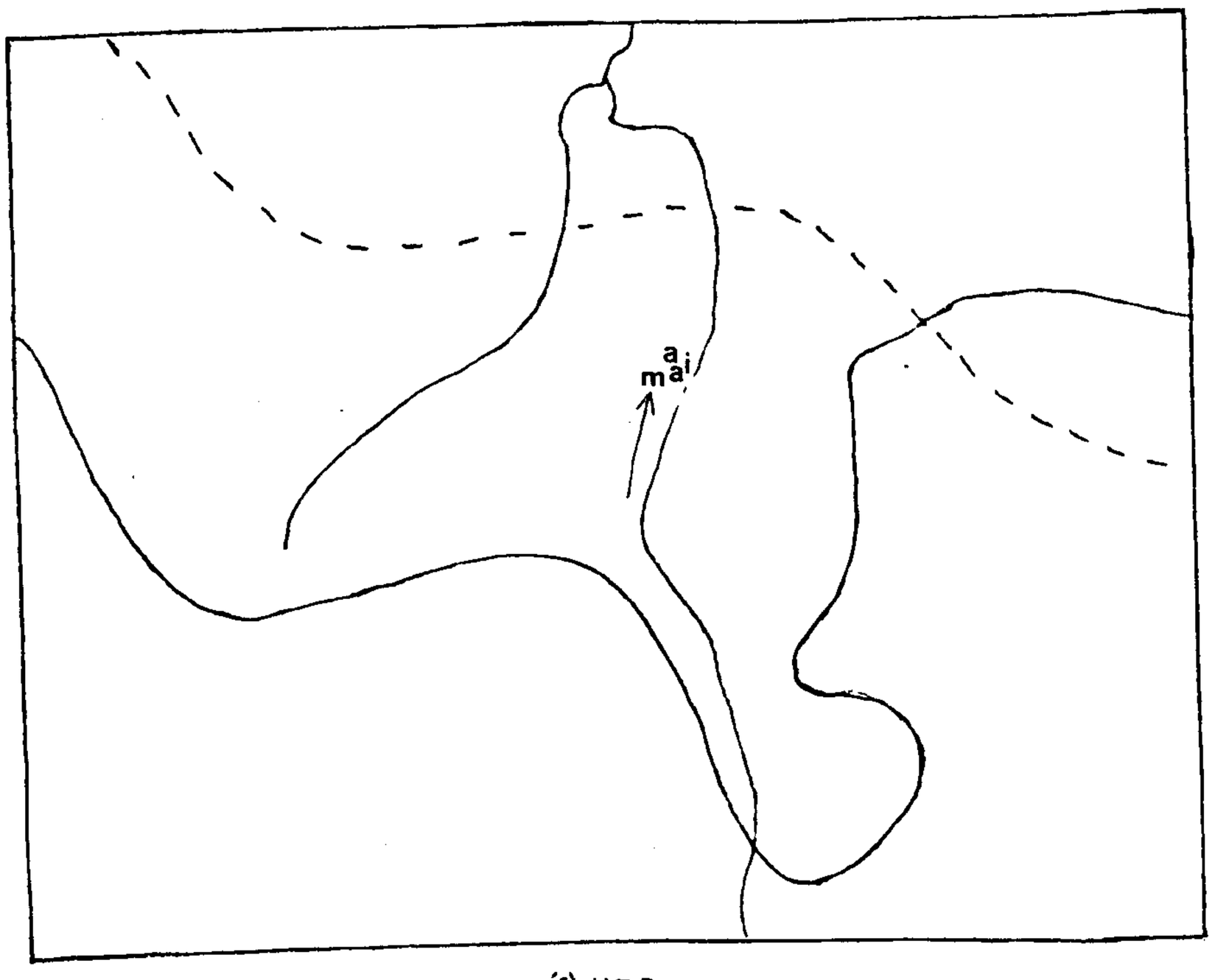


(d). 1030.

FIG. 3.6 (cont.)

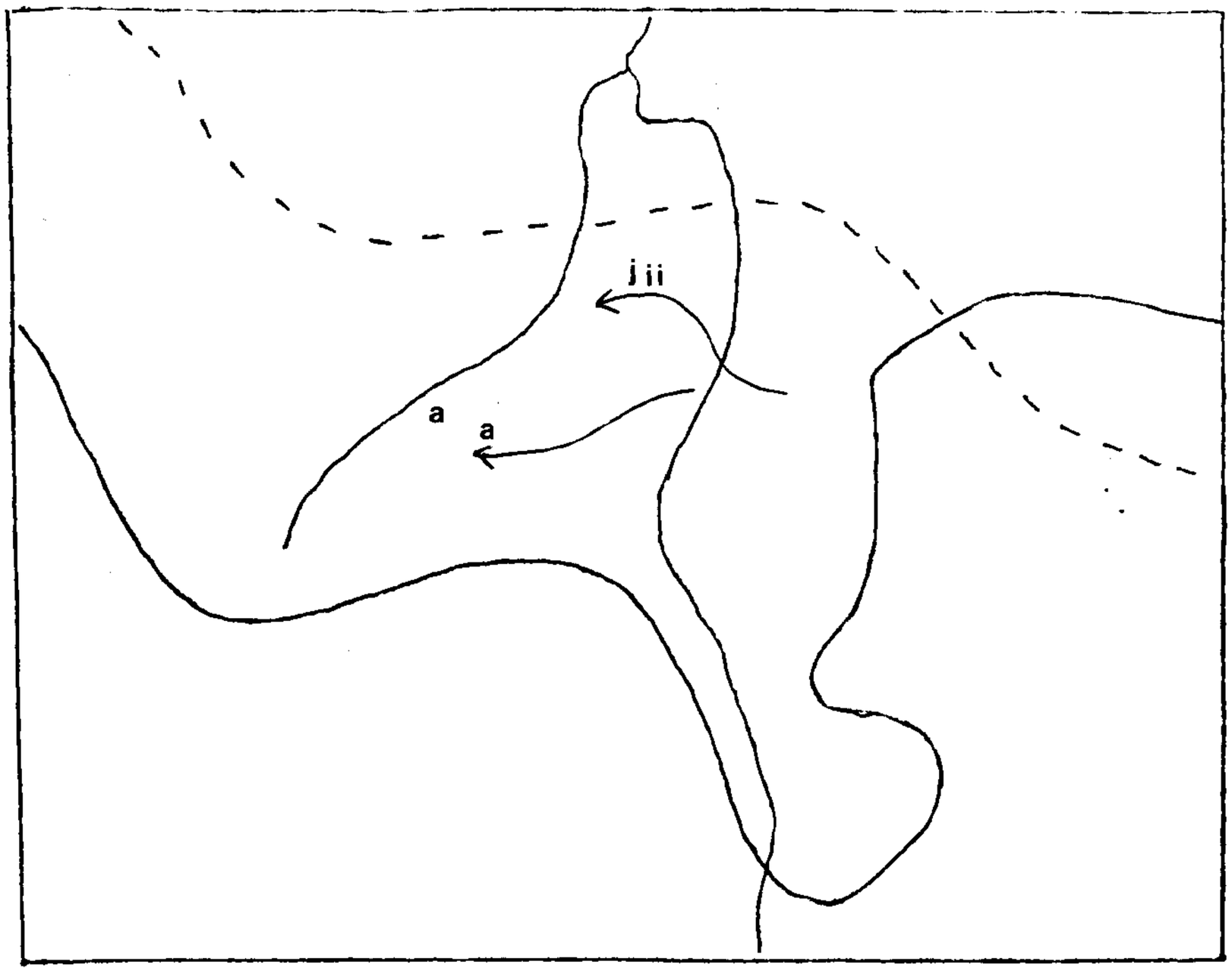


(e) 1100

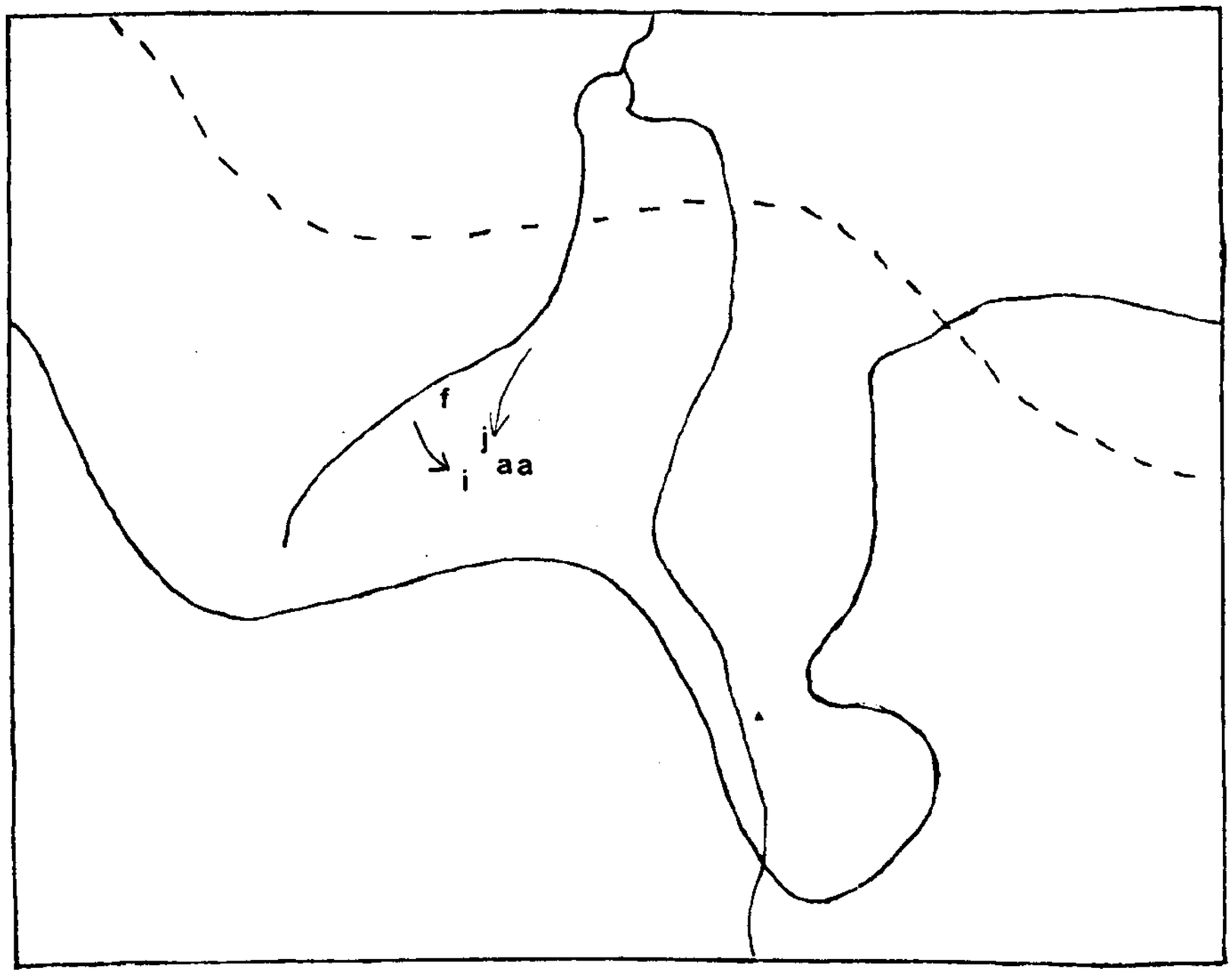


(f) 1130

FIG. 3.6 (cont)

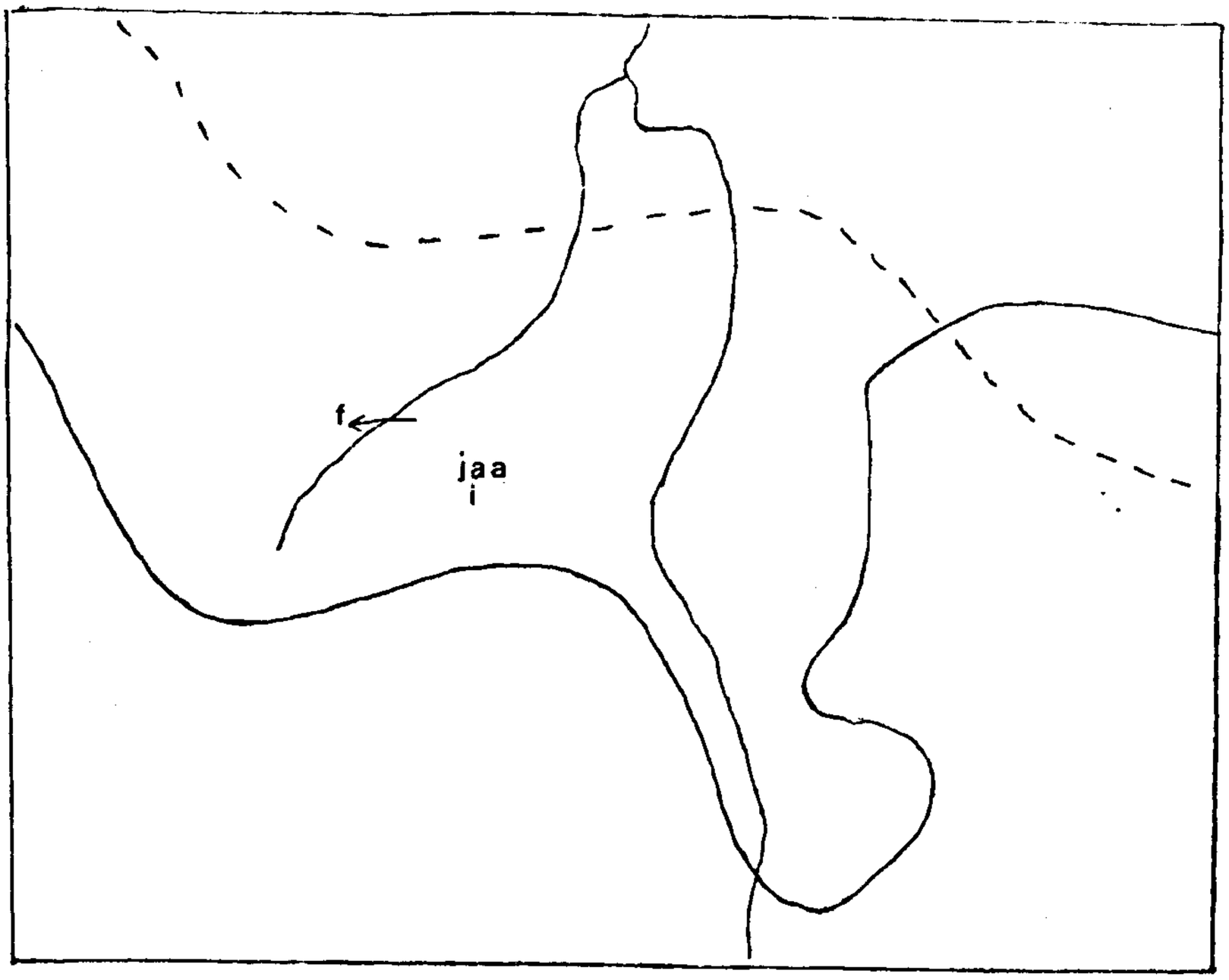


(g) 1200

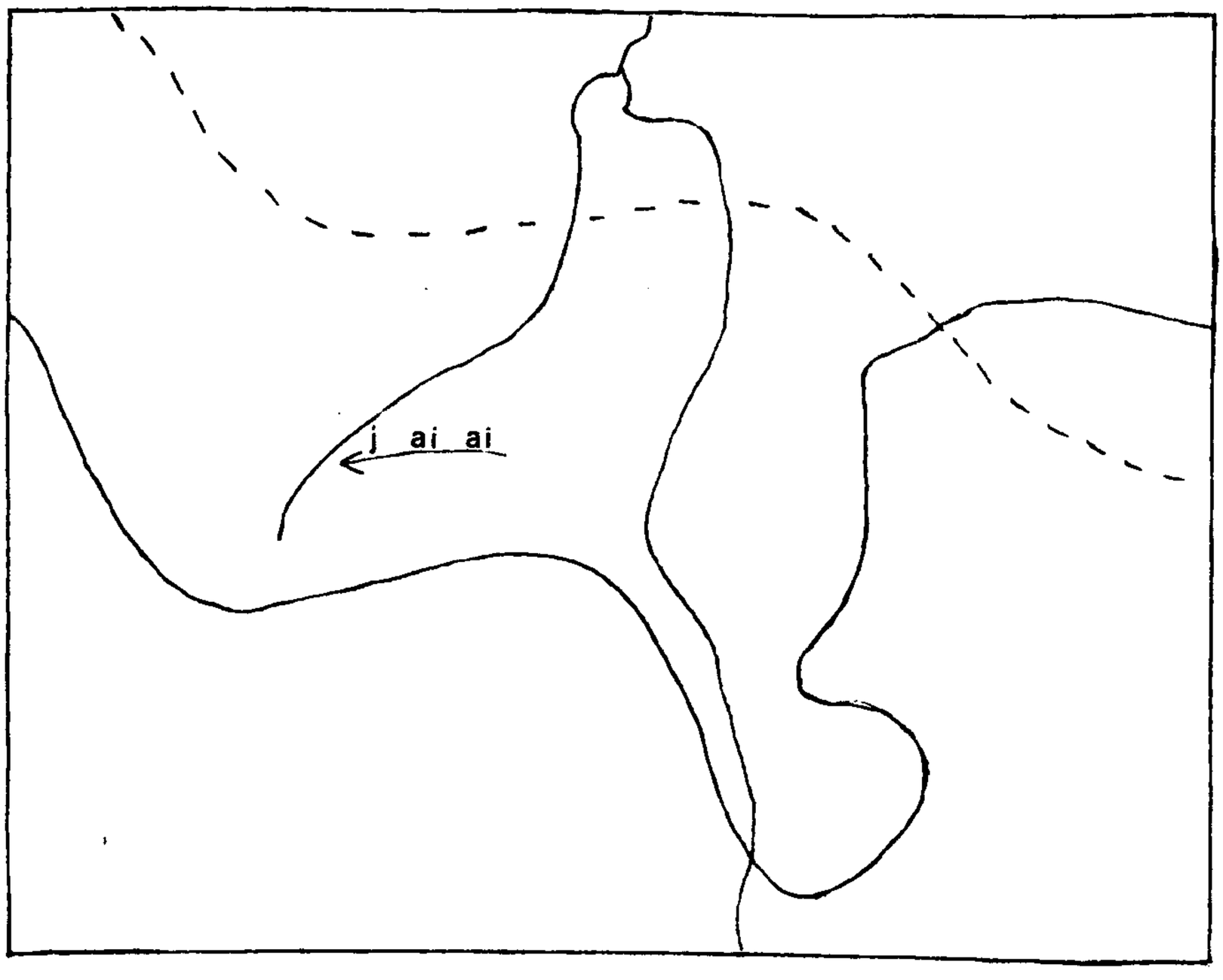


(h) 1230

FIG. 3.6 (cont)

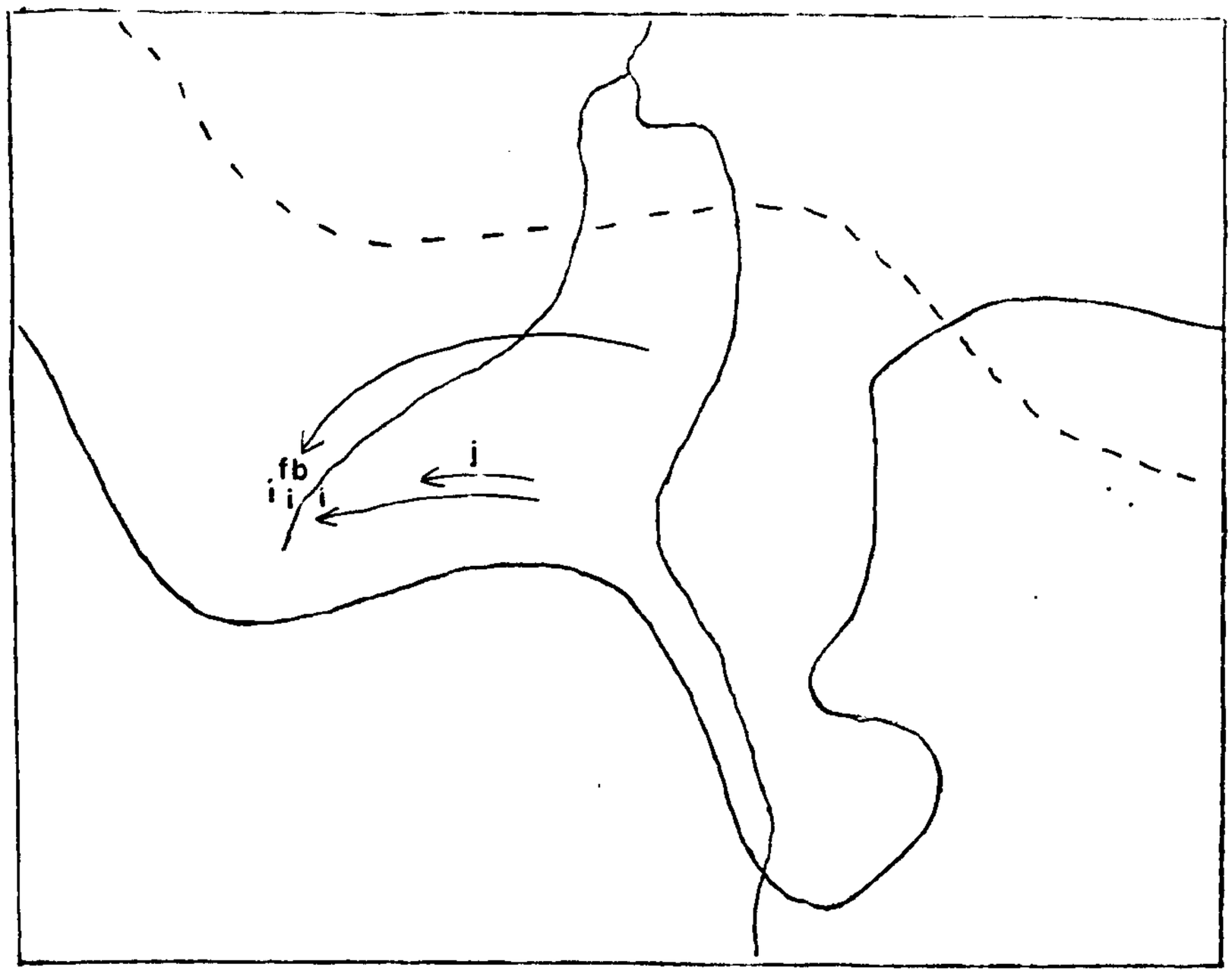


(i) 1300

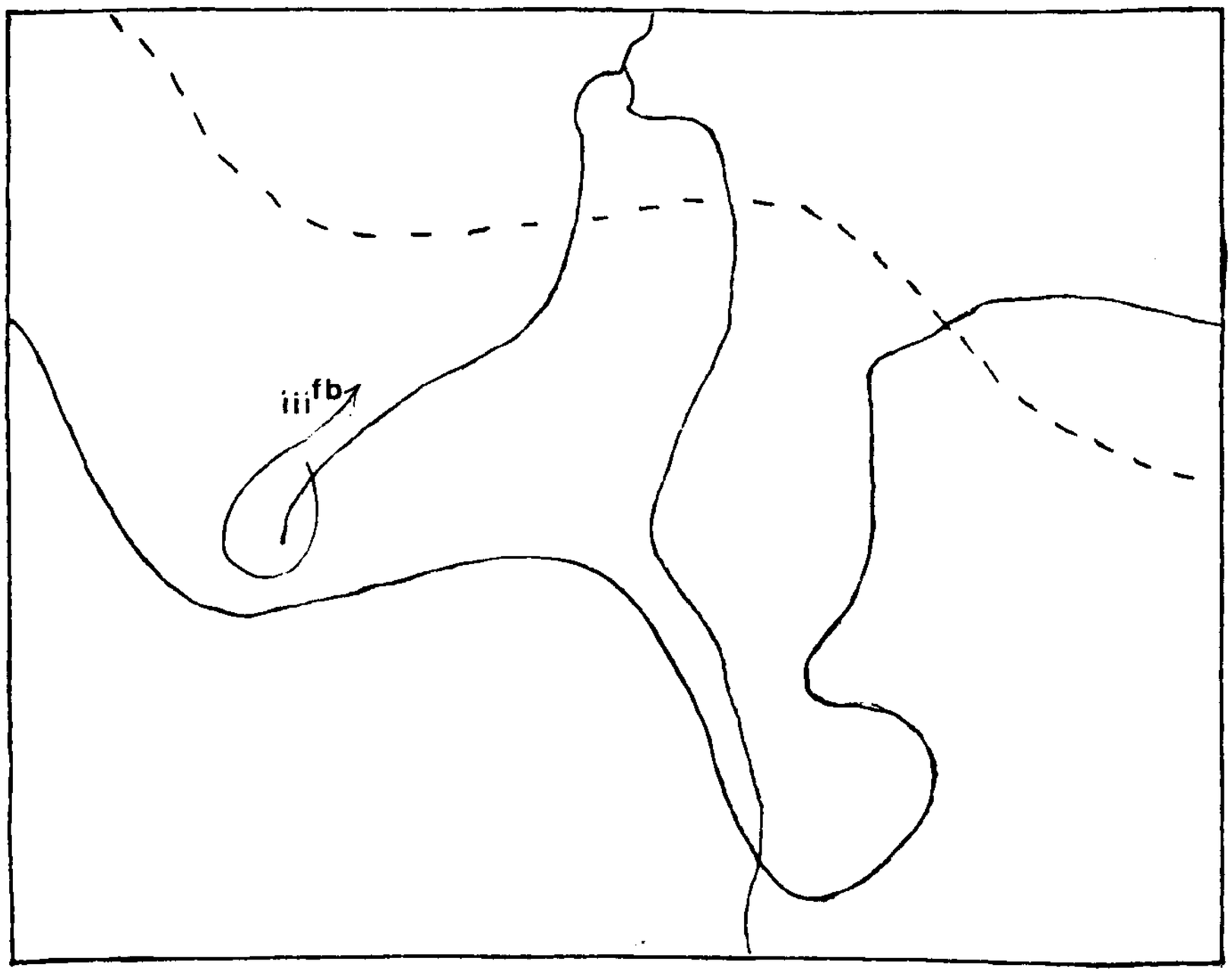


(i) 1330

FIG. 3.6 (cont.)



(k) 1400



(l) 1430

less straight line in any direction. There is thus less regularity in the routes used when moving about in this type of forest.

The series of maps in fig. 3.6 show the positions of monkeys at half hour intervals, and observed movements in the previous half hour, on the morning of Oct. 6th, 1966. The number of monkeys on succeeding maps does not necessarily correspond; animals would appear or vanish without one being able to see where they had come from or were going to, and only a proportion of those in the vicinity of the observer would be visible at any one time.

On this morning, monkeys were first located in the fruiting fig tree, but at 0745 at least 8 moved out and away across the eastern stream when a party of chimps moved up into the same tree. They dispersed widely in the vicinity of the Funtumia trees, becoming spread over at least 100 yards. 10 individuals were seen here. By 0945 the chimps had left the fig tree, and at 1000 three monkeys moved back into it. They were joined at 1020 by four more, and at 1040 by a further one. Two others, including the mature male, failed to reappear at this stage. Between 1045 and 1050 six moved out of the fig tree and away across the stream, but two of them returned after 5 minutes. At 1105 the mature male appeared from upstream and moved into the fig tree. At 1150 two monkeys moved out of the fig tree and away towards the western stream, and 5 minutes later three more, presumably those that had disappeared across the stream to the east at 1045, were seen moving in the same direction but 150 to 200 yards from the first two, on the opposite side of a clearing. The two parties gradually coalesced, and other monkeys appeared in the same area. Between 1305 and 1355 all drifted slowly away into the valley of the western stream. At 1335 they were joined by

a female carrying a baby, which had not been seen so far that morning. Most disappeared into thick foliage above the stream, but some at least subsequently moved off again downstream at 1430.

It is clear from this example that the group does not move as a compact, coordinated unit. Group B probably contained 13 or 14 animals at the time, yet at any one moment the locations of only a third to two thirds of them were known, and these were sometimes spread over 150 yards or more. Those members of the group that were visible were frequently seen to move independently of one another.

There is nevertheless extensive overlap in the parts of the range used by the various individuals during the morning; they differ more in the timing than in the course of their wanderings. As already mentioned, this is due largely to the restricted location of food. When food is more scattered, groups become even more widely dispersed and small parties of monkeys from the same group move completely independently.

For example, on the morning of Jan. 14th, 1966 12 members of group C were located when still in their sleeping trees, spread over 75 yards in the S.W. corner of their home range. They fed together for half an hour, and then split into two parties. At least 6 monkeys moved away to the north across the road, while at least three remained on the southern side. When contact with the northern party was finally lost, the two were separated by a quarter of a mile.

This lack of group cohesion provides a striking contrast between the blue monkey and many other monkeys, particularly those living in open country. That it cannot be purely an artifact of the poor visibility is shown firstly by detailed observations such as those above, and secondly by the experience of other workers under forest conditions. Chalmers (1967, 1968a) had no difficulty in establishing the existence of discrete groups in the black mangabey; groups were very compact, seldom being spread over 50 yards, and individuals were seen apart from the group on only 10 occasions. Howler monkey groups are likewise compact (Chivers, pers.comm.), and the same appears to be true, though perhaps to a lesser extent, of Colobus guereza groups (Marler 1969a, Schenkel and Schenkel-Hulliger 1967, and pers. obs.). On the other hand Haddow (1952) could discern no discrete group structure in the redtail, and my own observations on this species suggest that its social structure may be similar to that of the blue monkey. Likewise Thorington (1967) found that a troop of 18 squirrel monkeys, Saimiri sciureus, moved ad a compact unit very little of the time, but foraged rather as small parties of perhaps 5 to 8 individuals.

In contrast groups of open country primates

generally move in a coordinated fashion (e.g: Papio anubis in savanna habitats, Hall and DeVore 1965, but see Rowell 1966 and Crook and Aldrich-Blake 1968 for accounts of this species in less open habitats). The total spread of a group may be large ... patas groups, for instance, are commonly spread over 300 to 500 yards (Hall 1965) ... but in open country it is much easier for the monkeys to keep in contact with one another and individuals or parties seldom move independently. The adaptive significance of the blue monkey's pattern of dispersion is considered further in the following chapter.

SLEEPING HABITS.

Considerable difficulty was experienced in determining the exact location of sleeping sites. The monkeys did not settle down for the night until after sunset when the light was fading rapidly. Under such conditions a moving monkey can usually be seen, but not one that is sitting still unless it is silhouetted against the sky. Similarly monkeys that had slept in thick foliage would not be readily visible in the early morning until after they had left their sleeping positions and started to move around. Hence although the general area in which a party of monkeys

slept might be known, details of numbers of monkeys in each tree, position in the canopy, and so on, were difficult to come by.

Such observations as were made revealed considerable variation in sleeping habits. Sometimes monkeys that had been feeding together would all move into the same tree to sleep, while on other occasions they would remain scattered over a wide area. They might sleep at any height from 30 ft. to 120 ft. above the ground, and on broad branches or among thin twigs or tangles of creepers.

For example on the evening of 25/10/66 a party of 9 monkeys from group C were feeding, spread over 50 yards, in the middle canopy. At 1810 a mature male and a female moved up into a large mahogany 30 yards from where they had been feeding, and between 1825 and 1855 they were joined by two more females, another adult, and two infants. These 7 settled down on big branches 100 to 120 ft. up, immediately below the umbrella-shaped canopy of the mahogany. The two remaining monkeys, a juvenile and an adult, disappeared into thick foliage in the middle canopy 30 yards from the others. Between 1845 and 1855, when it became too dark to see, there was little movement. Two female/infant pairs were sitting in contact with tails intertwined, and a third female and the male within two feet of one of these pairs (see fig. 3.7a). At first light the next morning the monkeys were seen to have moved but little during the night (see fig. 3.7b). The two female/infant pairs had spent the night together, as had the male and the third female. The remaining adult appeared to have slept by itself. Of the three sleeping pairs two had spent the night in forks in the branches and the third in a large kink in a branch.

In contrast, on the evening of 28/10/66 a party of 8 monkeys from group C were feeding in the middle

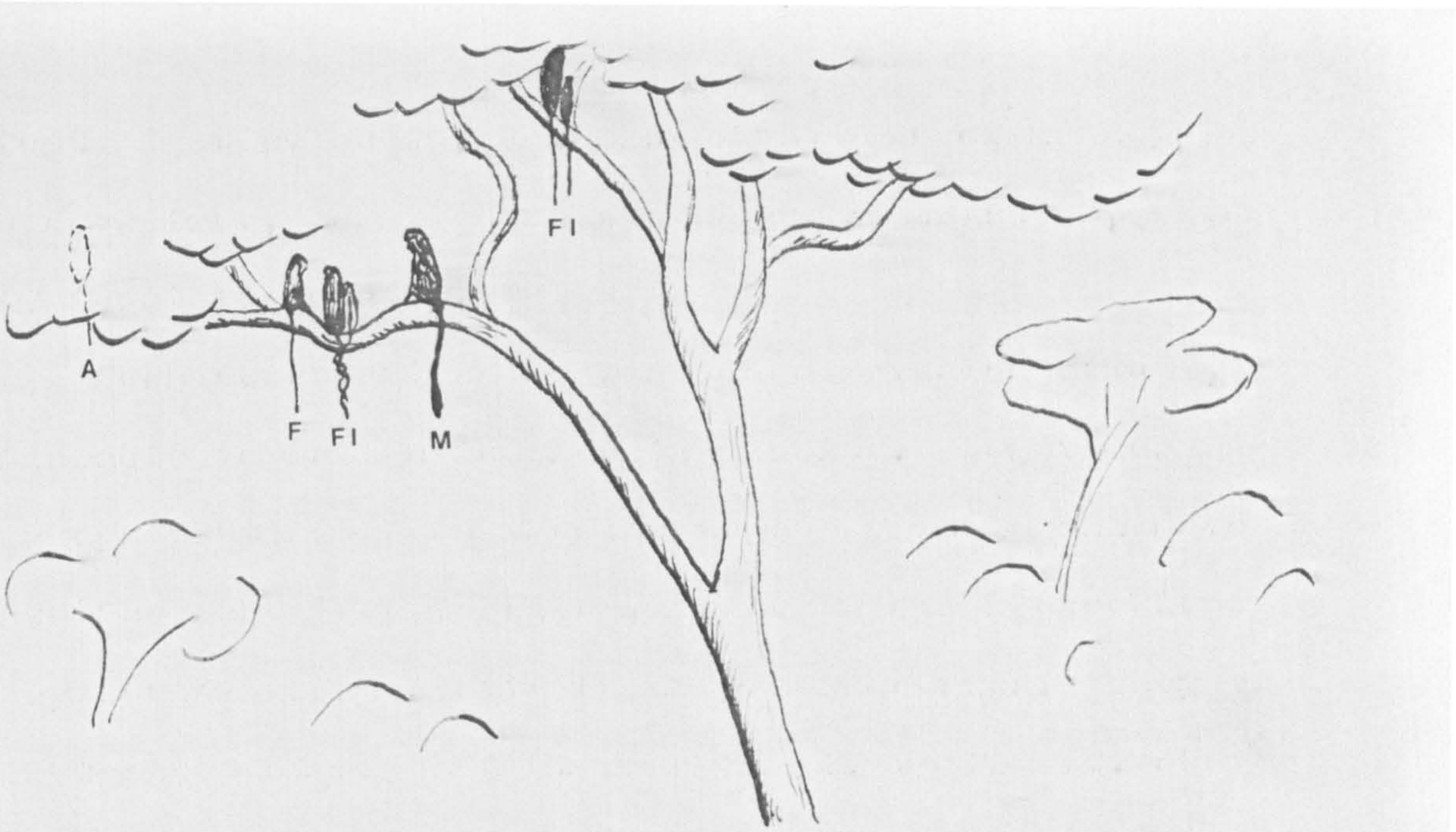


FIG. 3.7(a). POSITIONS OF MONKEYS AT DUSK ON 25/10/66.

(b). POSITONS AT DAWN ON 26/10/66.

KEY. M..mature male. F..female. A..unsexed adult. I..infant.

canopy. At 1745 a male and another adult moved away from the rest of the party and disappeared. The other 6 remained active, apart from 20 minutes during rain, until 1845, when they settled down for the night in the trees that they had been feeding in. At this time they were spread over 50 to 60 yards, and including the two animals that moved away earlier the original party of 8 would have been spread over more than 100 yards. Only two could be seen clearly enough to establish their exact sleeping positions; a female and an infant slept together 40 ft. up in small branches in a Funtumia tree.

As this latter example suggests, there are no regular sleeping trees; rather the monkeys spend the night in the area in which they have been feeding during the evening. In this respect they resemble the black mangabeys studied by Chalmers (1967); in all of the 11 cases of night resting that he observed the mangabeys slept in the same locality as they had been feeding in that evening. On the other hand Lumsden (1951) suggests that in the Semliki forest some species may have preferred sleeping trees. Gartlan (1966) found that the semi-terrestrial C.aethiops of Lolui Island would sleep anywhere within their territory where there was suitable cover ... the island abounded with small thickets and clumps of trees ... and they tended to sleep in the area in which they had been feeding in the last half hour of daylight. In contrast many terrestrial species such as baboons have but few sleeping sites in their range and return to them night after night (DeVore and Hall 1965). Presumably the most important attribute of a

sleeping site is that it should provide a refuge from potential nocturnal predators. In forest many trees in a group's home range would fulfil this requirement, so one would not expect to find regular sleeping trees. Indeed there might be an advantage in avoiding sleeping in the same place on successive nights; predators would have less opportunity to learn the location of sleeping monkeys.

Detailed records of sleeping sites were obtained on 14 nights. The number of monkeys sleeping in a single tree ranged from one to seven, with a mean of 4.0 (s.d. = 2.2). In Semliki Lumsden (1951) recorded 15 'night resting bands' of blue monkeys of mean size 3.5 (s.d. = 1.8, range 1 - 8). Precisely what is meant by a band in this context is not clear; it is most probably the number of monkeys in one tree, but could refer to 'huddles' of monkeys sleeping in contact. Comparison of the 17 single tree parties observed in the present study with Lumsden's data on night resting bands does not reveal any significant difference between the means of the two samples ($t = 0.654$, $p => 0.1$). Within each tree, the monkeys slept singly or in pairs; babies and infants slept with their mothers whereas other adults and juveniles almost always slept alone.

Species of tree used for sleeping included Albizia sp, Chlorophora excelsa, Cola cordifolia, Cordia milleni, Cynometra alexandri, Entandophragma sp, Ficus natalensis, Funtumia elastica, Guarea sp, Maesopsis eminii, and Mildbraediodendron excelsum. No tree was seen to be used more than twice. The parties observed by Lumsden used 8 different trees, of 6 species. Some trees were used more than once, but the small number of records did not permit any conclusions as to the existence of regular sleeping sites.

ACTIVITY AT NIGHT.

No evidence was found for any extensive activity at night. In cases when monkeys were seen to take up their sleeping positions in the evening and were located again at dawn the next day, they had never moved more than a few feet during the night. Haddow (1952) did not observe copulation in the redtail, and so concluded that this and other Cercopithecus spp. must copulate at night. There does not appear to be any direct evidence for this assertion, and blue monkeys certainly mate during the hours of daylight. Alarm calls were heard at night on two occasions, once at about 0300 hrs at the same time as baboon alarm

barks, colobus 'roaring', and leopard coughing, and once at 0445 hrs during a severe earthquake.

Chapter 4

DIET AND MOVEMENTS IN RELATION TO FOOD SUPPLY.

DIET

Methods of investigation.

All records of diet were obtained by direct observation; the shooting of monkeys to obtain samples of stomach contents was not practicable, and the identification of material so collected would in any case have presented considerable problems. A small amount of faecal matter was examined, but did not add anything to what was already known about the diet.

Identification of forest trees was far from easy; tropical forest contains a bewildering variety of species, and since the larger trees have no branches on the lower part of the bole all the foliage is well out of reach and it is difficult to obtain samples of leaves or fruit. One has to rely on picking up fallen leaves from the forest floor and examining the canopy with binoculars to see if they match those growing on the tree concerned. However some trees have a characteristic 'slash'; if the bark is cut with a panga the colour, texture, and smell of the inner layers so revealed and any exudate from the cut may suffice to identify the tree. Whenever possible the identity of trees was checked with Forest Dept. personnel on the spot, and in more

problematical cases samples were taken to the Forest Dept. headquarters at Entebbe for further confirmation and comparison with herbarium material.

Composition.

The diet of blue monkeys consists mainly of fruit, (in the wider sense of the word), young leaves and shoots, buds, and flowers, supplemented by occasional insects and other arthropods. Old leaves were eaten in quantity only when nothing else was available. The monkeys were not seen to eat bark, though they sometimes chewed moss or lichen growing on it. Likewise no evidence for the eating of birds' eggs, fledglings or small mammals was obtained.

Species of tree used for food are listed in fig. 4.1. The list is not exhaustive, but contains most or all of the more important species. It refers only to the main study area in Budongo; there may be considerable contrasts in diet between monkeys living in regions of different floristic composition. Most of the monkeys' food was provided by less than 30 species, of which they ate the fruit, or seed pods of 25. This gives a somewhat exaggerated impression of the proportion of fruit in the diet, since in the case of the many unidentified species

Fig. 4.1 Food plants of the blue monkey

Species	Part eaten	Importance*
Albizia coriaria	flowers	C
Albizia zygia	flowers, seed pods, young shoots	A
Albizia glaberrima	flowers, seed pods, young shoots	C
Alstonia boonei	young shoots, leaves	C
Aningeria altissima	fruit	A
Antiaris toxicaria	fruit	B
Balanites wilsoniana	young shoots	C
Caloncoba schweinfurthii	flowers	C
Celtis wightii	fruit	B
Celtis durandi	fruit, young shoots	A, C
Celtis zenkeri	fruit, young shoots	A, C
Chlorophora excelsa	young leaves	C
Chrysophyllum albidum	fruit	C
Chrysophyllum perpulchrum	fruit	C
Cola gigantea	young leaves, fruit	B, C
Cordia milleni	young leaves, flowers fruit	B, C, B
Croton machrostachyus	fruit, flowers	B, C
Cynometra alexandri	young shoots, leaves young seed pods	B
Dichrostachys glomerata	green seed pods	C
Entandophragma angolense	green seed capsules, young leaves	A, C
Entandophragma cylindricum	green seed capsules, young leaves	A, C
Erythrina abyssinica	flowers	C
Ficus capensis	fruit, young leaves	B, C
Ficus depauperata	fruit	C

* A .. more than 50% of one group's diet at some period.
  B .. frequently eaten
  C .. eaten only occasionally

(cont'd)

Fig. 4.1 Food plants of the blue monkey

Species	Part eaten	Importance*
Ficus exasperata	fruit	C
Ficus mucoso	fruit	B
Ficus natalensis	fruit	A
Ficus stipulifera	fruit	A
Ficus sp. indet.	fruit	C
Funtumia elastica	green seed pods, seeds	A
Funtumia latifolia	green seed pods, seeds	A
Harungana madagascariensis	fruit	B
Khaya anthotheca	young shoots, flowers	B, C
Maesopsis eminii	fruit, leaves	A, C
Mildbraediodendron excelsum	young shoots, fruit	B
Morus lactea	fruit, young shoots	A, C
Olea welwitschii	fruit	B
Parkia filicoidea	flowers, seed pods	C
Phoenix reclinata	fruit	C
Phyllanthus discoideus	fruit	C
Pseudospondias microcarpa	fruit	A
Pygeum africanum	fruit	A
Ricinodendron heudlotii	young leaves	C
Sapium elipticum	fruit	C
Schrebera arborea	young seed capsules	B

* A .. more than 50% of one group's diet at some period.

B .. frequently eaten.

C .. eaten only occasionally.

used for food only occasionally it was generally leaves and shoots rather than fruit that were eaten. 60-70% fruit and 30-40% other matter would be a more accurate assessment.

Most fruits were eaten when still unripe by human standards. In some cases, for instance the seed capsules of Entandophragma spp. or Schrebera arborea, this is presumably because the capsules become too hard when mature. On the other hand there is an obvious advantage in eating fruits at an early stage in their development before some other animal eats them instead. Moreover as Rowell (1966) has pointed out, the protein content of many fruits is probably higher at this stage than when they are fully ripe.

In addition to the trees listed in fig. 4.1, the berries of at least two species of creepers and climbers were commonly eaten and the flowers and shoots of such plants figured frequently in the diet. Mosses and lichens were sometimes eaten, though it was not always clear whether it was the plants themselves or insects in them that provided the attraction.

Haddow (1956) states that blue monkeys do not raid native crops. On the other hand Booth (1962) regards members of the C.mitis group in Kenya as crop raiders. The incidence of the habit is probably

dependent more on opportunity than anything else. In Budongo monkeys have little chance for such depredations as there are few areas where shambas come right up to the forest edge. However Mr. R.G. Knight of Busingiro tells me that blue monkeys sometimes enter his garden, some 200 yards from the edge of the forest, to raid fruiting mango and banana trees.

Though blue monkeys are predominantly vegetarian the diet is often supplemented by insects and other arthropods. Identification of the species eaten was seldom possible, but ants probably figured prominently among those taken; ants of various species swarm everywhere at ground level and penetrate at least 50 ft. up into the canopy, and indeed some may be exclusively tree living. Monkeys could often be seen picking objects off the bark, in rapid succession, and transferring them to the mouth with one hand. Sometimes a monkey would peer intently at a spot on the bark for a few seconds, and then make a sudden grab at it. This approach would be suited to the capture of winged insects.

Many species of tree, Cynometra for example, have bark which peels off in flakes; partially detached flakes commonly conceal insects and other arthropods such as spiders and amblypygids. Monkeys would tear

FIG.4.2 A monkey peeling flakes of bark off the trunk of a Celtis tree.

off flakes of bark and sieze creatures from underneath them (see fig. 4.2). Epiphytic ferns and other such growths also harboured insects; monkeys would search systematically through clumps of epiphytes and pick objects out of them. Likewise long streamers of Usnea lichen were pulled up from beneath the branches and searched through.

A juvenile monkey was once seen to put its hand into a wild bees nest, though whether by accident or design was not clear. It thrust its hand deep into a hole in a tree, whereupon a swarm of bees emerged and buzzed round it. It sat swatting at them for half a minute, then apparently was stung and leapt away.

For a few days in March and April 1966 large numbers of termites, Macrotermes sp, were swarming in the grasslands surrounding the forest. After a brief nuptial flight the males and females fell to the ground to shed their wings. On bare earth, for instance on a road or track, they could be picked up by the score. Where a road passed near the forest edge monkeys would emerge from the forest to feed on them. These were the only occasions on which blue monkeys were seen on the ground in any numbers.

Drinking.

The monkeys were occasionally seen to lick drops of rain off leaves, or run a hand along underneath thin branches to collect drops

of water hanging there and then lick it off the hand. On one occasion a juvenile hung upside down sloth-like from a branch and licked drops of water direct from underneath it. Drinking was rare, however, and the monkeys must obtain most of their liquid requirements from their food.

Drinking was observed in Cercopithecus cambelli by Bourlière, Bertrand and Hunkeler (1969), and in Cercocebus albigena by Chalmers (1967, 1968a), but as with the blue monkey neither of these species drank regularly. Haddow (1952) states that no East African monkey other than Papio is known to drink in the wild; certainly this would seem to be the only species to drink at all often.

SEASONAL VARIATIONS IN FOOD SUPPLY.

Outside the forest there are marked seasonal changes in the vegetation, related to the alternation of wet and dry seasons. Within the forest, however, there is no such clear cut correlation. While there are changes in the vegetation during the course of the year, they are often on a different time scale to the climatic cycle and are not necessarily related to it. For instance while many trees lose their leaves at

the beginning of the dry season others shed them in the middle of the rains, and some of those species that lose them early in the dry season put out new shoots well before the rains recommence. Khaya, Albizia, and Cordia trees, for example, had young leaves on them in January 1967, but the rains did not begin until mid March. Likewise trees of at least some species were fruiting at almost any time of the year.

Unfortunately the Forest Dept. had only just started to collect systematic data on fruiting seasons when I was in Uganda, but such information as is available indicates that there is considerable variation in pattern both within and between species. Individual trees may follow an annual cycle, or a regular cycle of lesser duration such as eight months, or they may fruit at irregular intervals. All the trees of a particular species in an area may fruit at the same time, or fruiting may be unsynchronised. For example, in late August and early September 1965 all the Maesopsis trees in the study area were fruiting heavily, but only a few fruited at this time in 1966. A heavy crop of fruit started to develop on the rest in December 1966, but did not finally ripen until March 1967. Similarly a particular Ficus mucoso fruited in

December 1965, September 1966, and February 1967. On the other hand a Pygeum africanum fruited in February in both 1966 and 1967, and all specimens of Albizia zygia in the study area flowered at much the same period in both years. Almost all the Pseudospondias microcarpa in the forest fruited in June 1966, and regular annual synchronised fruiting may be typical of this species in Budongo; Reynolds and Reynolds (1965) record it as fruiting in June 1962 when they were in Budongo. On the other hand at Ishasha, 200 miles further down the rift valley, Rowell (1966) found that while individual Pseudospondias trees followed a clear cycle fruit could be found at almost any time of the year.

The duration also of the fruiting season varies between species. Some fruits such as the seed pods of Funtumia spp take several months to develop. Others, like the fruits of Pseudospondias, ripen in a much shorter period. Some may remain on the trees for weeks, while others may fall within days. Fruits and young shoots may be palatable for only a short time during their development, as little as four days in some types of shoots.

The combination of all these factors means that feeding conditions do not follow a regular seasonal

fluctuation; rather they change on a much shorter time scale, in the region of one to three weeks. While a particular tree or group of trees are fruiting feeding conditions might remain relatively constant, but as the fruit is exhausted or other species start to fruit the pattern of food distribution changes. When the monkeys are feeding predominantly on young shoots the pattern alters even more rapidly, almost from day to day.

The detailed account below traces changes in the state of the forest over the 15 months from January 1966 to March 1967. To appreciate the way in which the pattern of food dispersion is continually shifting it should be considered in conjunction with figs. 4.3 and 4.4. In fig. 4.3 are plotted the locations of isolated feeding trees, and in fig. 4.4 the areas occupied by those species that commonly grow in clumps or groves rather than as isolated individuals. Fig. 4.5 summarises the monkeys' main sources of food throughout the study.

January 1966.

Olea welwitschii trees in group C's range were fruiting, as were a few Harungana madagascariensis trees on the forest edge and one by the side of the road in group B's range. A few Funtumia trees,

FIG. 4.3 LOCATIONS OF ISOLATED FEEDING TREES

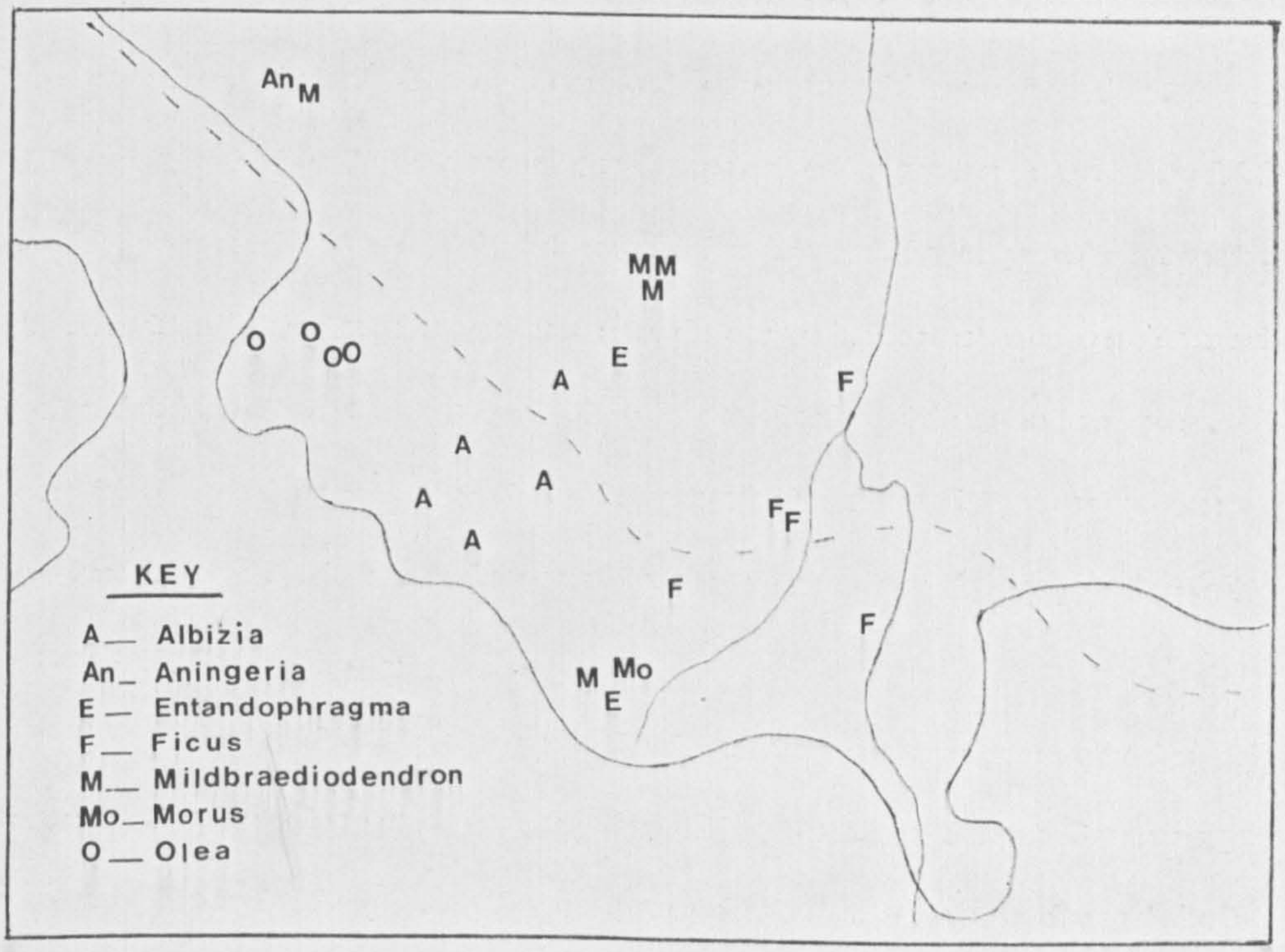


FIG. 4.4 LOCATIONS OF COMMON FOOD SPECIES

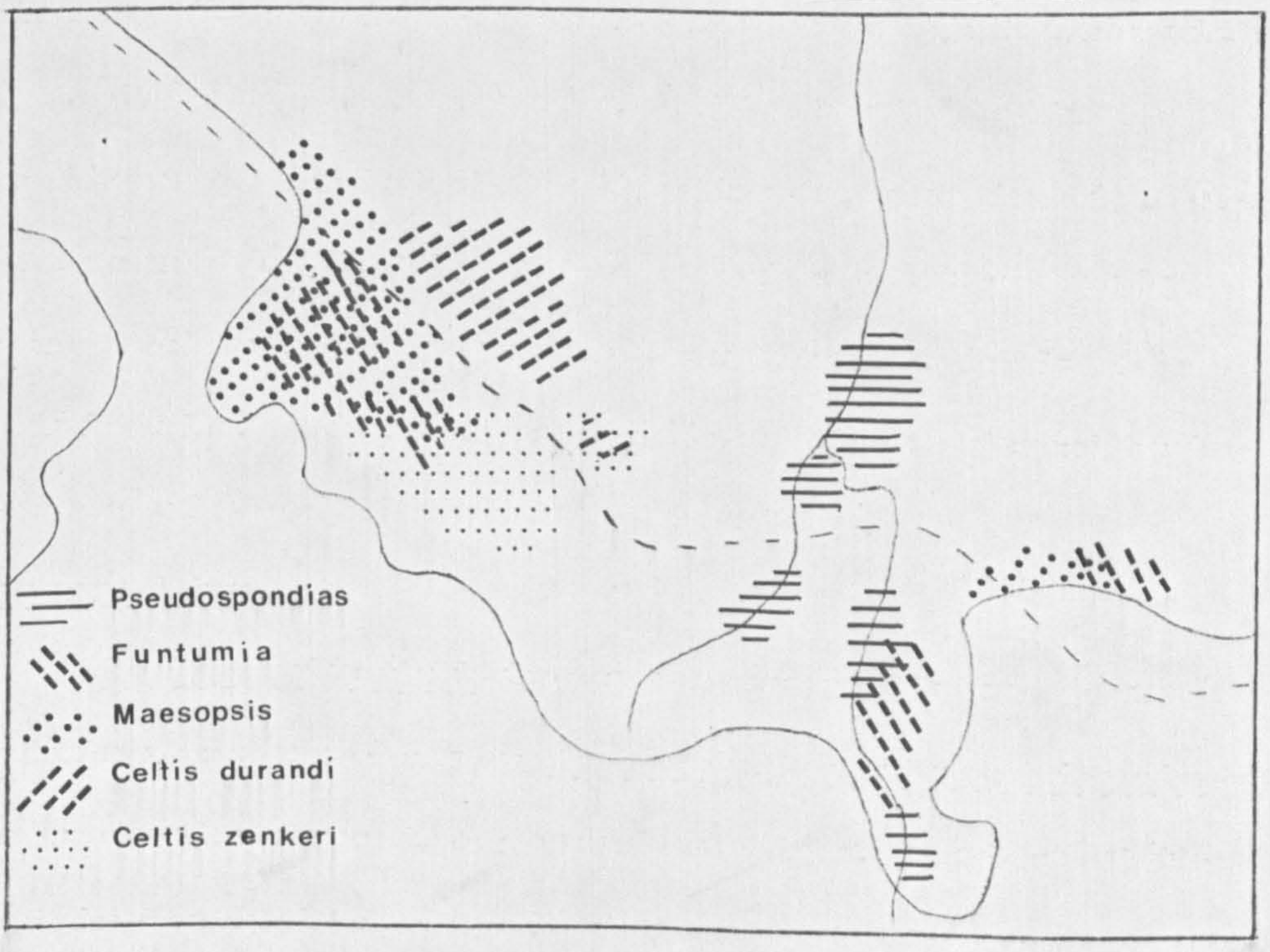


FIG.4.5 MAJOR SOURCES OF FOOD AT DIFFERENT SEASONS.

SPECIES	1965 AUG.	SEP.	OCT.	NOV.	DEC.	JAN.	FEB.	MAR.	APR.	MAY.	1966 JUN.	JUL.	AUG.	SEP.	OCT.	NOV.	DEC.	1967 JAN.	FEB.	MAR.
ALBIZIA CORIARIA																		oOOOOo		
ALBIZIA ZYGIA							fFFFFFFFf		oOOOo											
ANINGERIA ALTISSIMA											FF									
ANTIARIS TOXICARIA																			ffFF	
CELTIS DURANDI														fffffffffffff						
CELTIS WIGHTII														fFFFFFFFf						
CELTIS ZENKERI												fFFFFFFf								
CORDIA MILLENI											FFFFFFFFFFFf									
CROTON MACHROSTACHYUS									OOOO		FFFFFFFFFFFf									
ENTANDOPHRAGMA SPP.											FFFFFFFf									
FICUS SPP.									FFF					fffffffffffff				fffff		
FUNTUMIA SPP.							FFFFFfffff							fffffffffffffffffffffffffffff						
MAESOPSIS EMINII	FFFF																	ffFFF		
MILDBRAEDIODENDRON EXCELSUM											FFF									
MORUS LACTEA									fFFf											
OLEA WELWITSCHII							FFFFFf													
PSEUDOSPONDIAS MICROCARPA											FFFF									
PYGEUM AFRICANUM							fFFFFf												fFFFFFf	
SCHREBERA ARBOREA														ffFFFFFFFFf						
YOUNG LEAVES OF VARIOUS SPP.						LL	LLLLLLLLll											LLLLLlllll		

NO OBSERVATIONS, 3/9/65 - 7/12/65

NO OBSERVATIONS, 21/4/66 - 3/6/66

KEY: Ff... flowers. Oo... leaves. Ll... leaves. Large letters... eaten frequently, small letters... eaten occasionally.

FIG.4.7 Albizia pods.

FIG. 4.6 Two adults, a juvenile, and one other, partially hidden by foliage, eating Funtumia pods.

FIG. 4.8 A mature male eating young Albizia shoots.

FIG. 4.6 Two adults, a juvenile, and one other, partially hidden by foliage, eating Funtumia pods.

FIG. 4.8 A mature male eating young Albizia shoots.

scattered widely throughout colonising forest, had mature pods on them (see fig. 4.6). For a few days in the middle of the month young shoots of small Khaya trees in group C's range were eaten intensively. Towards the end of the month Albizia zygia pods figured prominently in the diet of groups C and D. (see fig. 4.7). The grasslands surrounding the forest were dry and by the end of the month most had been burnt, but the forest itself was not particularly dry.

February.

Albizia zygia pods were still eaten intensively during the first part of the month, but by its end they were hard and papery, though individual seeds were still picked out of them occasionally. In group D's range the emphasis of feeding shifted to a fruiting Pygeum africanum. For the last two weeks several trees had buds and young shoots on them, and Albizia shoots in particular were often eaten (see fig. 4.8). Food was widely dispersed with no major concentrations, as were the monkeys themselves. Showers of rain were more frequent than in the previous month.

March.

Throughout the month many species of tree had

young shoots on them, and these were a major item of diet. In the second half of the month Albizia zygia, Khaya anthotheca, and Croton machrostachyus trees were flowering; the flowers of the first species were eaten intensively, and those of the latter two occasionally, by monkeys in groups C and D. A single Morus lactea in group B's range provided a focus of attention for this group. At the end of the month fruit on a Ficus mucoso in group A's range was ripening, and monkeys were beginning to feed selectively on the riper fruits. Several palm trees, Phoenix reclinata, in the wetter part of the study area had fruit on them, but this species did not appear to be greatly favoured by the monkeys. The rains were by then well under way, and the undergrowth in the forest was becoming more rank.

April.

There were still many trees with buds and young shoots, and these continued to figure prominently in the diet. Albizia zygia flowers were eaten during the first part of the month, as were Croton flowers. Several Funtumia trees were flowering, but the flowers were not seen to be eaten. The Ficus mucoso in group A's range was entirely stripped of fruit by chimpanzees during the first week. The month was very wet, and

parts of the Kamirambwa valley were under water.

(May... no information available).

June

Pseudospondias trees in the swamp forest in groups A and B's ranges were fruiting heavily; monkeys and chimps fed on them throughout the month and by its end they had been almost stripped of fruit. A large Aningeria altissima on the boundary of groups E and F's ranges was fruting early in the month, but the fruit was exhausted after a week. Several Entandophragma cylindricum and E.angolense had heavy crops of green pods. Cordia milleni, Cola gigantea, Croton machrostachyus, and Trichilia prieuriana trees were fruiting, and small Albizia trees were flowering. Towards the end of the month fruit on a group of Mildbraediodendron excelsum ripened sufficiently to be eaten by the monkeys.

July

Green Entandophragma pods still figured prominently in the diet, particularly of group C, in the first half of the month, but by its end they had become too hard for the monkeys to tackle. Cola, Cordia, Trichilia and Croton trees were still fruiting. Maesopsis trees flowered early in the month, and a few small Ficus trees had fruit on them though not in

sufficient quantity to be a major attraction to the animals. A Phyllanthus discoideus in group C's range fruited early in the month. The forest was becoming rather dry.

August

Small pods were beginning to develop on Funtumia trees, and a few Maesopsis had a very light crop of fruit beginning to ripen. Several Cynometra had young pinkish-yellow leaves on them, but these did not appear to be so attractive to the monkeys as young shoots of other species and they were eaten only occasionally. Harungana trees on the forest edge were flowering. Celtis zenkeri trees, a particularly common species in groups C and D's ranges, had much fruit on them early in the month. I was unable to be in Budongo during the latter half of the month, but before I went away monkeys had started to feed on these Celtis fruits and by the time I returned early in September all had been completely stripped. It therefore seems likely that they were an important item of diet.

September

Early in the month there were no major sources of food, though a few Cordia still had fruit on them and some trees had young shoots. By the end of the

month the situation had changed; a very heavy crop of fruit had ripened on a Ficus natalensis in group B's range and provided a focus of attention for them. Though there was no such concentrated source of food in other groups' ranges, Funtumia pods were beginning to be eaten and fair numbers of Celtis durandi were starting to fruit. A Schrebera arborea in group A's range had green seed capsules on it.

October

The Ficus natalensis in group B's range continued to provide food for most of the month, and towards the end a Ficus stipulifera in group A's range was fruiting heavily and attracted both blue monkeys and chimps. There was a very heavy crop of Celtis durandi fruits and Funtumia pods in areas of colonising forest, and at the end of the month Celtis wightii trees were fruiting also. Food appeared to be more abundant than at any other time of the year.

November

For most of the month food was still very abundant. Celtis durandi fruits were exhausted early in the month, but there were still plenty of Funtumia pods and Celtis wightii fruits. Albizia glaberrima trees were bearing pods. The first part of the month was very wet, but the second half was dry and by its

end the undergrowth was beginning to wilt.

December

All Celtis fruit was exhausted. The Funtumia pods were becoming hard and only the seeds, not the pods themselves, were eaten. Olea trees at the western end of the study area were flowering, and most Maesopsis had fruit developing though the fruits were still green, hard, and very small. The forest was becoming rather dry, and some trees had lost their leaves.

January 1967

The forest was very dry and the grasslands surrounding it were burnt. More trees had shed their leaves, but during the course of the month Khaya, Cordia and Albizia trees put out new shoots. Shoots and buds formed the greater part of the diet, and as the young leaves took only a few days to open beyond the stage at which they were eaten the pattern of distribution of food changed almost daily. Most Funtumias had dry, dehiscing pods on them, and the seeds were eaten. Parkia filicoidea trees were flowering, and flowers from a specimen in group A's range were eaten occasionally. Albizia coriaria trees on the forest edge started to flower at the end of the month.

February

The forest was still very dry. Albizia zygia, Albizia coriaria and Khaya trees were flowering, and flowers and young shoots still formed a major part of the diet. The Pygeum africanum in group D's range was fruiting. Funtumia seed was still available.

March

The Maesopsis fruit finally ripened, and was eaten intensively. There did not appear to be any other major sources of food, though a few small Albizia trees had buds and an Antiaris toxicaria in group B's range was fruiting. Seed pods on the Parkia filicoidea in group A's range were eaten occasionally. For the first part of the month the forest was still dry, but a heavy storm on the 14th heralded the end of the dry season.

DISPERSION OF MONKEYS IN RELATION TO FOOD SUPPLY.

During the course of the study I gained a strong impression that the pattern of dispersion of the monkeys was intimately connected with the abundance and distribution of food. To demonstrate the relationship between feeding conditions and dispersion, ideally the location and quantity of all potential sources of food and all the monkeys should be plotted, and the

relation between them evaluated statistically. In practice this is not possible.

Firstly, one cannot tell where all the monkeys are all the time; one can plot only the location of some of the monkeys some of the time, and these may represent only a small proportion of the whole group. Secondly, one cannot map the distribution of all the available food. It cannot be said whether a potential food is in fact edible until one has seen monkeys eating it. Certain fruits, those of Trichilia prieuriana for instance, were never seen to be eaten by monkeys, but this does not necessarily mean that they were wholly inedible. They might merely have been less favoured than other sources of food available at the same time. Even with a complete knowledge of the range of plant species usable for food, one would still have great difficulty in mapping food resources. Small fruits and flowers are easily overlooked, particularly those of upper canopy species, and often the presence of feeding monkeys is the first indication that a tree is bearing food. Quantitative estimation of the available food in any one tree would present further problems. It is clear, therefore, that the best that can be achieved is a broad outline of feeding conditions rather than a detailed quantitative assessment.

Within these limitations, however, a clear relationship between feeding conditions and monkey dispersion can be demonstrated. It has already been shown, in Chapter 2, that the apparent size of parties of monkeys varied with feeding conditions. Though estimates of the pattern of food availability were qualitative rather than quantitative, contrasts between the different patterns are considered sufficiently clear for such an approach to be valid. It was found that small parties were the rule both when food was scarce and widely scattered and when it was abundant and widely distributed, but larger parties occurred when food sources were rich and localised. From this it was inferred that the total spread of the group and its degree of fragmentation were dependent on variations in feeding conditions.

If this conclusion is correct, maps of the locations of monkeys during periods of contrasting feeding conditions should reveal differences in dispersion. Figs. 4.9 - 4.11 show the distribution of all monkeys sighted during three ten day periods of contrasting feeding conditions. They should be considered in conjunction with figs. 4.3 and 4.4 which give the location of feeding trees. Each dot represents a single monkey in that region for half an hour;

FIG. 4.9

DISPERSION OF MONKEYS IN THE STUDY AREA, 15/1/67 - 24/1/67.

See text for explanation.

FIG. 4.10

DISPERSION OF MONKEYS IN THE STUDY AREA, 27/9/66 - 7/10/66.

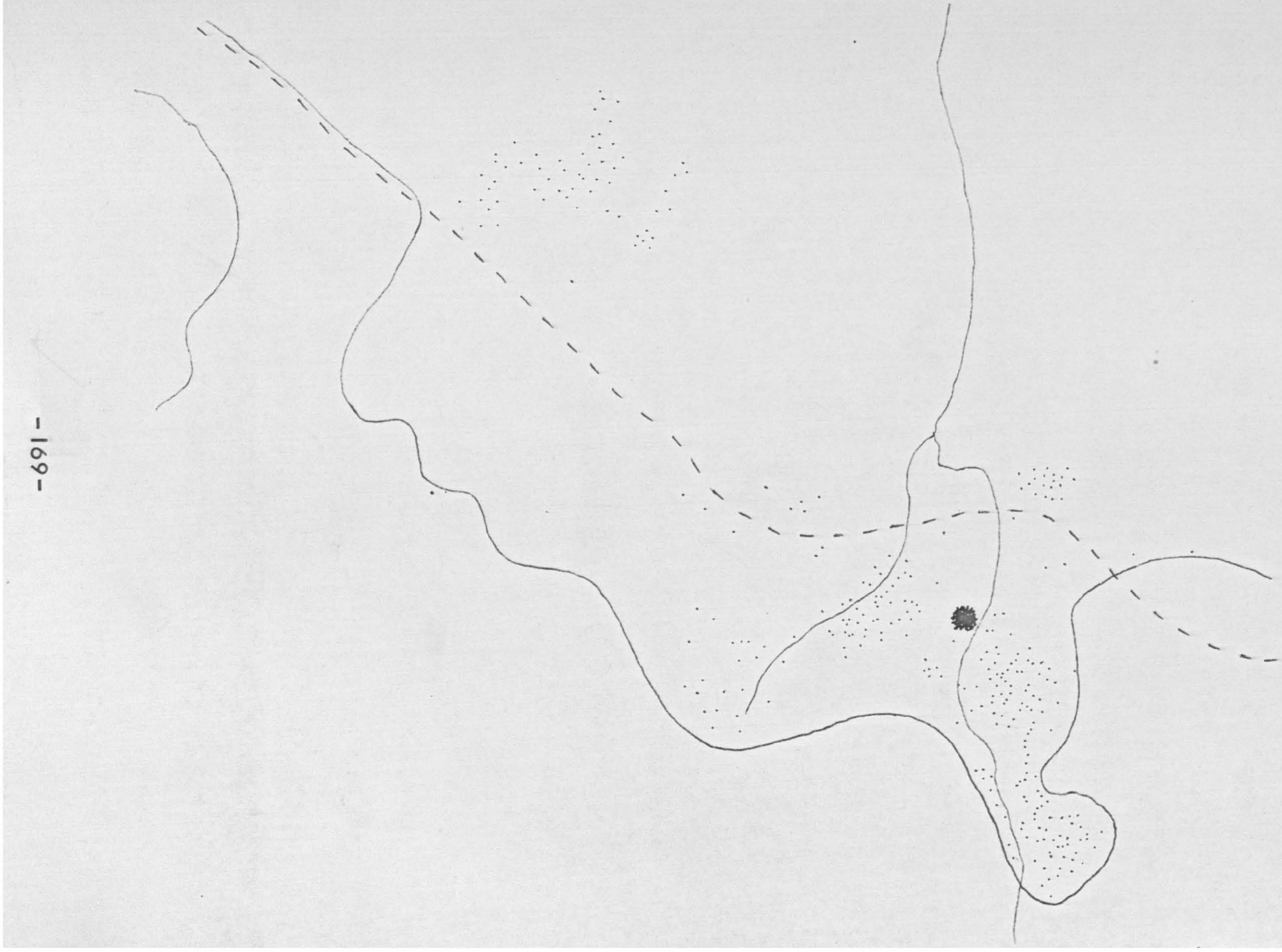


FIG. 4.11

DISPERSION OF MONKEYS IN THE STUDY AREA. 23/10/66 – 1/11/66.

thus a party of 12 monkeys watched for half an hour would be represented by 12 dots scattered over the area they were seen in, as would a party of 4 monkeys watched for 1½ hours. Since not all parts of the study area were sampled equally but observations concentrated rather on a single group for a few days at a time, the maps do not give an overall picture of dispersion throughout the area. Within those parts of the area visited frequently, however, the pattern that emerges should be reasonably accurate.

During the period 15/1/67 - 24/1/67 covered in fig. 4.9 most observations were concentrated on group D. At this time the monkeys were feeding on young leaves and shoots. Food was widely scattered and its distribution changed almost daily. Fig. 4.9 shows that the monkeys also were widely dispersed. Virtually the whole area of the home range was used during the period and there were no concentrations of activity in particular parts.

Fig. 4.10, covering the period 27/9/66 - 7/10/66, shows a contrasting situation. At this time most observations were on group B. Within this group's range there was one very rich, concentrated source of food, a Ficus natalensis with a heavy crop of fruit. In addition a few Cynometra and Funtumia trees to the

west and south east of the fig tree bore small amounts of food. While much of the range was used at some time during the period, there was a massive concentration of activity in the fig tree, and most of the records for other parts of the study area were of monkeys visiting the two subsidiary food sources mentioned above.

Fig. 4.11 shows the situation a fortnight later. Much of the fruit on the F.natalensis had been exhausted, but the few contacts made with group B during the period showed that there was still a tendency for activity to centre on this tree. In group A's range a fruiting Ficus stipulifera provided a similar attraction, as the concentration of records to the north of the road shows. Most observations during the period, however, were made in group C's range, where a third type of feeding condition prevailed. Common understory trees, in particular Celtis durandi, were fruiting heavily. Food was therefore abundant and widely distributed. It can be seen that group C remained widely scattered, the pattern of dispersion being similar to that of group D in fig. 4.8 when food was scarce. The two situations differ, though, in that much of group C's range was apparently unused during the period, while

group D, at a time of food scarcity, covered most of its range. Though group C was widely dispersed it did not move far from the main sources of food.

It seems reasonable to conclude that not only is the dispersion of each group within its range very variable, but that variations in dispersion are indeed closely related to feeding conditions. Taken as a whole, the evidence indicates that under typical conditions the group would be spread over perhaps 200-250 yards, with small parties moving to some extent independently, but that when food was localised the monkeys would aggregate within a smaller area.

DISCUSSION.

Flexibility in dispersion could be considered of adaptive value in the exploitation of a continually shifting pattern of food resources. Independent foraging of widely scattered parties would result in the range being searched more efficiently than if the whole group were to move around as a compact unit. The chances of small, localised sources of food being discovered would be increased, and the possibility of conflict over minor concentrations insufficient to feed more than a few monkeys reduced. On the other hand the mobility of the foraging parties and the

small size of the home range should ensure that the whole group became concentrated on rich and localised sources of food if there were no alternative supplies.

Aggregation at such feeding sites might be assisted by other factors. Unlike chimps, which are more dependent on rich food sources such as fruiting fig trees and range over a wider area, blue monkeys are no more vocal than usual on finding food. However, the location of fruiting trees was obvious from some distance, to the human observer at least, as a result of the calls of other frugivorous creatures such as hornbills; it seems probable that the monkeys also might make use of such cues. It is also possible that they might remember the locations of feeding sites over a period of days, and perhaps even from season to season, though the lack of regularity in fruiting seasons and small area of the range would not place very great premium on such a capacity.

An analogous alternation between large 'herds' and smaller 'one male groups' under different feeding conditions is found in the gelada (Crook 1966), and chimpanzees in Budongo show similar flexibility (Reynolds and Reynolds 1965, Sugiyama 1968a, and pers. obs.). Likewise Gartlan (1966) found that vervet groups on Lolui Island were more dispersed in their

territories towards the end of the dry season, when fruit was scarce and other types of food figured prominently in the diet, than at other times of year. Gartlan's data on day ranging patterns indicate that the spread of the group varied greatly; at times a group might be scattered over a large part of its range. The pattern of dispersion is thus not unlike that of the blue monkey. (Group size and range are similar also in these populations of the two species).

Flexibility in dispersion within discrete groups has not been described explicitly in other open country species, but such flexibility would be less striking under observational conditions that allowed the whole group to be seen at the same time and hence might escape comment. On the other hand factors such as the risk of predation might be expected to promote group cohesion in open country, and hence prevent fragmentation even if feeding conditions were such as to render it advantageous. It is perhaps significant that the Lolui vervets had no terrestrial predators; vervets at Amboseli, where predators were numerous, lived in compact groups (Struhsaker 1967 c).

If these arguments are correct, one might expect flexibility in dispersion to be relatively more frequent in forest than in open country species. To

date too few forest species have been studied in sufficient detail for us to know whether this is so. C.ascanius appears to have a flexibility similar to that of the blue monkey (Haddow 1952, Buxton 1952, and pers. obs.) as does Ateles geoffroyi (Carpenter 1935). On the other hand mangabey and howler groups are, as noted in the previous chapter, compact. The existence of compact groups in forest habitats does not, however, invalidate the argument that flexibility is an adaptation to a shifting pattern of food resources. The various forest monkeys very probably exploit different aspects of the habitat, and patterns of food availability may differ from one niche to another.

Chapter 5

SOCIAL BEHAVIOUR I. (Aspects of communication).

INTRODUCTION.

The existence of a society, as opposed to a mere aggregation of animals, presupposes some means of communication between the individuals that make up that society. At a particular level of analysis, the study of communication is therefore essential to the understanding of social behaviour.

Ideally any study of animal communication should include description of the circumstances leading up to and attending the production of a signal, the signal itself and its degree of stereotypy, and the reaction of other animals to that signal. In practice, as Marler (1965) has pointed out, these aims are seldom attainable even under favourable circumstances; in the poor conditions of observation typical of forest they are hardly ever realised. Like most other monkeys blue monkeys employ two main channels of communication, the auditory and the visual. In the case of vocal communication the signals themselves can readily be described but it is seldom possible to see the animal making them, let alone work out why it is making them or whether apparent reactions from other monkeys are responses to the signal itself or to other factors. For visual signals the problems are somewhat different; it is harder to observe the

signal in the first place, but if it can be seen the antecedent circumstances and subsequent results are generally clearer.

Studies of captive animals may facilitate accurate and detailed description of signals, but their value as an aid to the complete understanding of communication is limited. Firstly, captive animals may not give the whole range of signals that they do in the wild. Compare, for instance, Andrew's (1963) catalogue of Cercopithecus calls, derived from captive animals, with results from studies of these monkeys under natural conditions such as those of Gartlan (1966), Struhsaker (1967d), Gautier (1969), and the present work. Certain types of call, notably those involved in intergroup spacing and territorial encounters, and specialised responses to predators, are not mentioned at all in the captivity study.

Secondly, and more important, signals cannot be separated from the circumstances under which they are produced; the same signal may elicit different reactions under different circumstances. Or to use Smith's (1968) terminology, we may distinguish between the 'message', the signal or display itself, and the 'meaning', the interpretation placed on a message by the animals receiving it. Meanings are derived

' ... not simply from messages, but from messages in contexts.' (Smith 1968). Communication must, by definition, involve more than one animal; to concentrate solely on the signal itself without regard for its context cannot, therefore, give more than a partial understanding of the process. It follows that a full understanding of communication under natural conditions can only be attained by studying the animals under those conditions; the results of cage studies will not necessarily be applicable to the natural situation. While description of the finer details of certain signals has been facilitated by observation of captive monkeys, the conclusions which follow are based, unless stated to the contrary, on data obtained in the forest.

Vocal communication is discussed in the section immediately following. Visual and tactile signals are considered in subsequent chapters, but distributed amongst sections on categories of behaviour such as grooming, aggression and so on rather than as a topic in their own right. Thus while the classification of vocal signals is purely descriptive, that of other types of signal is contextual. Such a separation of the various types of signal is admittedly artificial, but is considered the most expedient way of presenting the available information.

As noted above, studies of vocal and visual communication present rather different problems. For vocal signals the context is often obscure, perhaps to the monkeys themselves as well as to the observer, whereas for visual signals it is as a rule not only relatively clear cut but also fairly restricted for each type of signal. For instance postures that have the effect of soliciting grooming are seldom if ever seen outside interactions that can be classified as grooming interactions. The approach adopted is hence more convenient than would be a unitary treatment of all types of signal.

CALLS.

(i) Volley calls

These calls are one of the two loudest made by blue monkeys, being audible at well over half a mile. They are normally given only by mature males, and hence by a single male in each group. Each call consists of a 'volley' of up to 30 units of relatively unstructured noise at intervals of about 0.3 secs, (see fig. 5.1). Series of up to ten such volleys may be given, with intervals of a few seconds between each volley. The sound is rather like a very loud and resonant football rattle played at half speed.

Detailed data are available on 47 series of volley calls, containing 143 individual volleys, (see fig. 5.2). The mean number of units in each call is 8.64 and the mean number of calls per series 3.14.

The antecedent circumstances to the making of volley calls were determined with some degree of confidence in 45 cases. By far the commonest situation was for volley calls to be given after volley calls from other monkeys. While the possibility that the animals concerned were reacting independently to some stimulus undetected by the observer cannot be excluded in every case, this is unlikely to be true of more than a minority. If one male started calling, others up to a third of a mile away might answer, and the two or sometimes three individuals would give a series of alternating calls. The number of volleys given by individual males tended to be greater during these exchanges than during unanswered series. (Means 3.42 and 2.79 respectively; Mann Whitney U test with correction for ties gives $p \leq 0.1$, two tailed). On four further occasions unanswered volleys were given during intergroup encounters. In five instances volley calls were made following the 'roaring' of black and white colobus, a call that appears to act as a spacing mechanism in this species (Marler 1969a).

Other situations in which volley calls were given included attacks by eagles (2) or their close proximity (2), and following 'explosive' calls (see below) from other males (1), claps of thunder (1), the crash of falling trees (1), and the appearance of the observer (1). Volley calls given in response to eagles were shorter than usual, and were made by several individuals in the group rather than by a single animal only.

Below are shown the numbers of volley calls heard during two hourly periods throughout the day, together with expected values, taking into account the varying amounts of time spent in the forest at different periods, were calls distributed evenly over the day:

Time:	7-9	9-11	11-1	1-3	3-5	5-7
No. of calls heard:	18	18	8	2	7	17
Expected number:	17	18.5	9.6	1.9	8.6	14.1

X^2 is 1.239 with 5 degrees of freedom, which is not significant. Hence although the raw data suggest at first sight that calls are more frequent in the morning and evening, this is wholly due to the fact that less time was spent in the forest in the middle of the day.

On 21 occasions parties of monkeys were sufficiently clearly visible for their reactions to volley calls to be recorded. Reactions were very variable, but could be placed in three categories. In 9 cases there was no obvious response at all. In two of these mature males were visible, but even they did not appear to react. In a further three cases monkeys merely looked in the direction of the call or made a quiet croak. In the second category, containing 6 cases, varying degrees of nervousness or alarm were shown. These ranged from looking in the direction of the call, scratching, and moving away slowly in the opposite direction to at once dropping out of the canopy and moving off at speed. In the remaining three cases the mature male in the party sat up as soon as the calls started and answered them, and in two instances he then moved off at high speed towards their source.

Marler (1968) has recently discussed primate communication in terms of its effect on spatial dispersion, and considers that many signals have the function of maintaining distance between groups. Examples of such signals are the howling of howler monkeys (Carpenter 1934, Chivers 1969), the roaring of black and white colobus (Marler 1969a), the calls

of gibbons (Carpenter 1940, Ellefson 1968), langurs (Jay 1965, Ripley 1967), Cercopithecus nictitans (Gautier 1969), and titi monkeys (Mason 1966, 1968), and perhaps the wailing of the indri (Petter 1965). However interchange of calls is in itself no evidence that the calls act as a spacing mechanism; only if the subsequent movements of the animals concerned bear this out can such a conclusion be justified (see, for example, Chivers 1969). The variability of the observed reactions to volley calls can readily be explained on such a basis. Responses depended not on the call itself or the distance of its source, but on the situation in which it was given. When adult males were seen to answer volley calls and move off towards them the animals they were answering sounded as if they were right on the edge of the observed male's range, or perhaps even a short way inside it. On the other hand when monkeys moved away from the source of volley calls they were themselves near the boundaries of their own ranges. When they showed little reaction they were well within their own ranges and the calls did not sound as if they were coming from near the boundary of the range.

(ii) Explosive calls.

Explosive calls are the second of the two loud calls made by blue monkeys. Like volley calls they are made only be mature males and by a single male in each group. Each call consists of a single explosive sound that could be rendered as 'pow' or 'kyuh'. Haddow (1956) describes it as sounding like a bursting tennis ball, but never having heard a tennis ball burst I cannot confirm the accuracy of this simile.

Spectrograms of explosive calls are shown in fig. 5.3. Analysis of ten such calls showed that their duration was on average 0.55 secs (range 0.4 - 0.6 secs), and the range of frequency covered extended to 5 KHz or above. The greater part of the energy was concentrated below about 2.6 KHz, and in the first 0.1 to 0.25 secs of the call.

The calls were generally given in series, at intervals initially of about 5 secs but increasing after the first few calls. The later calls in a series were shorter and not as loud as those earlier in the series, but apart from this there was very little variation in the calls, either for any one animal or between different individuals. 83 such series of calls were timed and counted. The number

of calls in each series ranged from one to 26, with a mean of 10.1 (see fig. 5.4). The mean duration of such series was 70.8 secs, and the longest series lasted three minutes.

The circumstances preceding the giving of explosive calls were determined in 51 cases. In 24 of these they were given in response to the observer's appearance, but not, however, as an immediate reaction. Typically the calls would start about a minute after the monkeys had seen me, and during this time individuals other than the male might be chirping (see below). The male might well have seen me and be looking at me, but would not start to call at once.

The next most common situation in which explosive calls were given was after volley calls from other monkeys. The two types of call were often associated; 24 out of 70 series or exchanges of volley calls included explosive calls also. In 22 of these the same male gave both volley and explosive calls, and in the 13 cases in which explosive calls were given in answer to volley calls the male giving the explosive calls made volley calls also.

Other situations in which explosive calls were given included the passing of cars or lorries on the

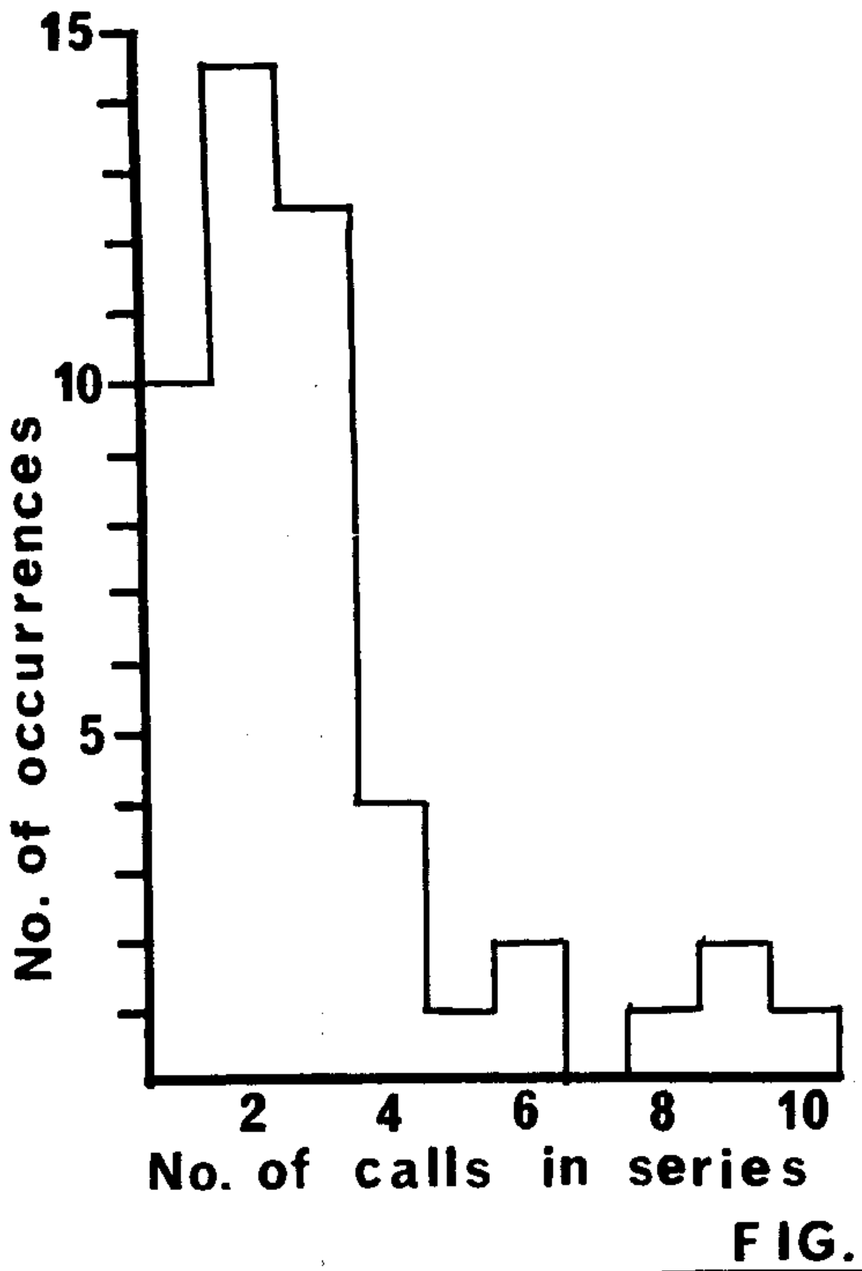


FIG. 5.2 VOLLEY CALLS.

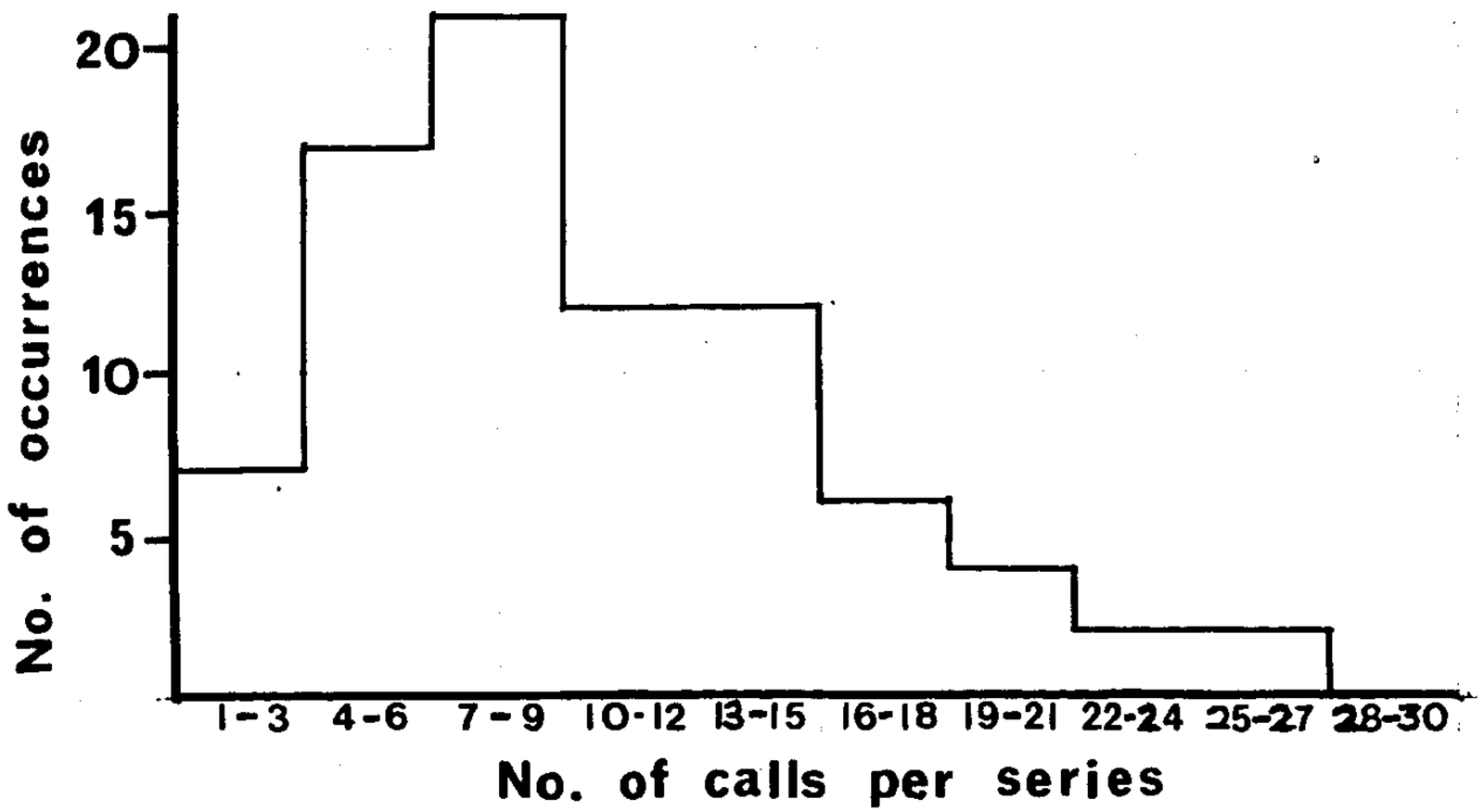
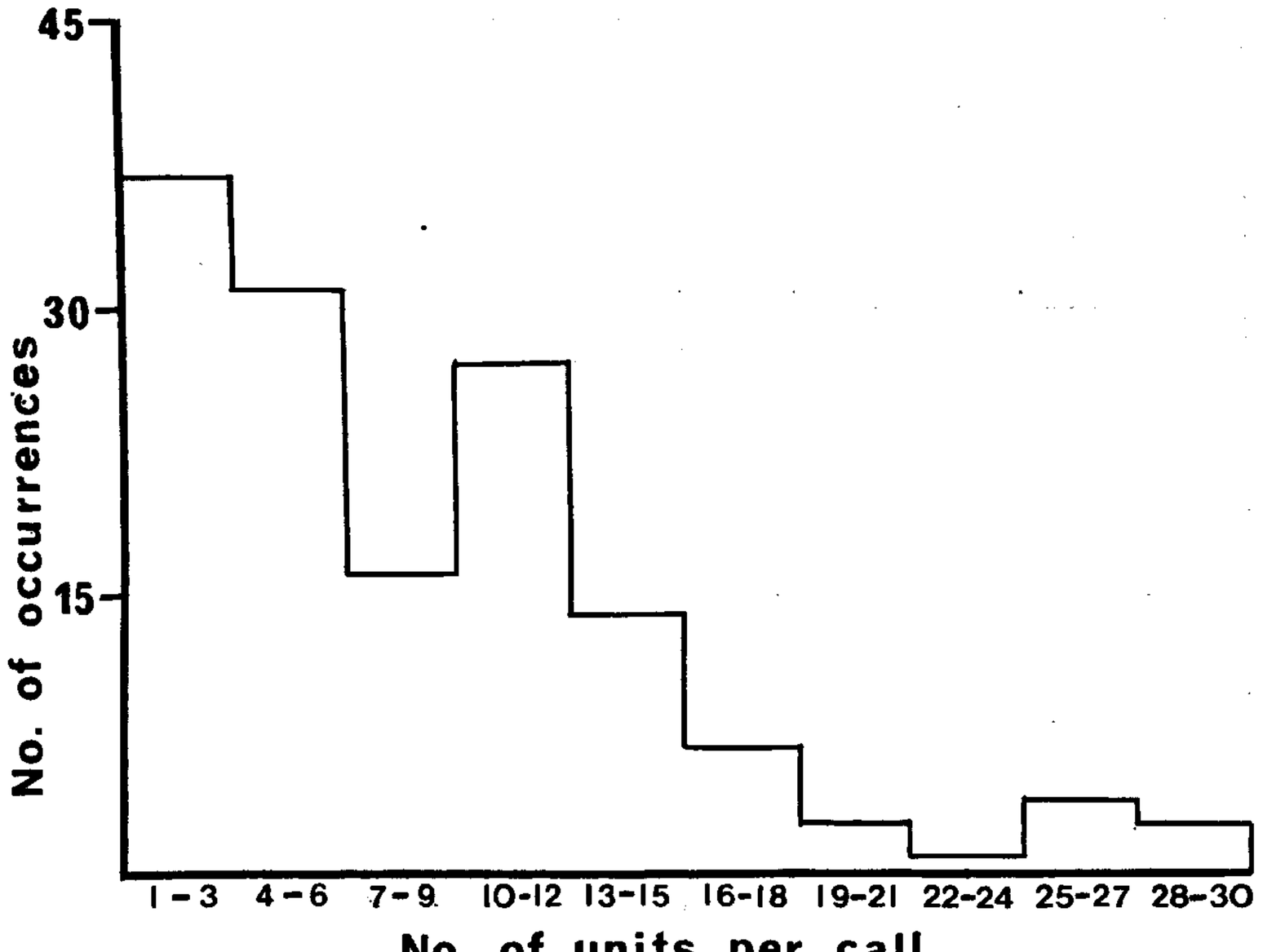


FIG. 5.4 EXPLOSIVE CALLS.



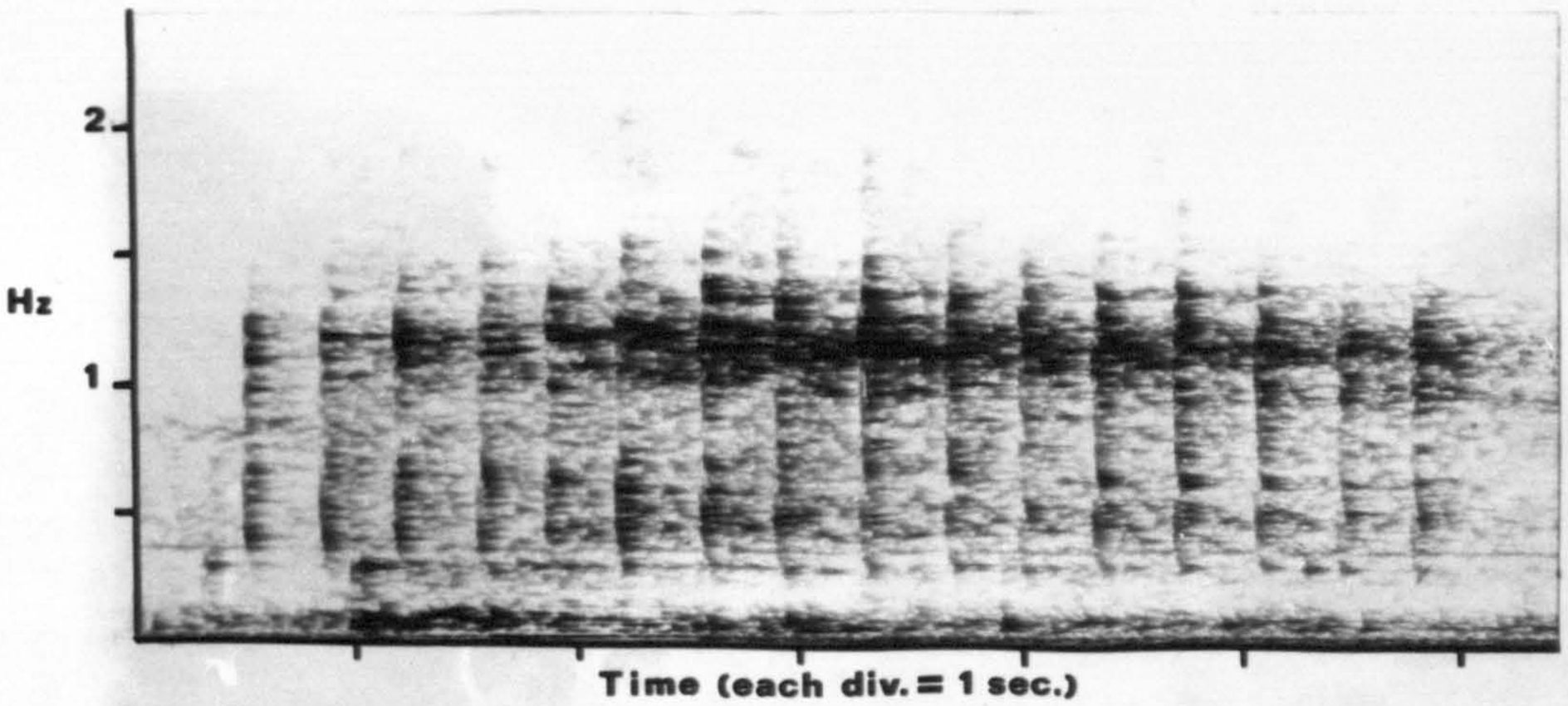
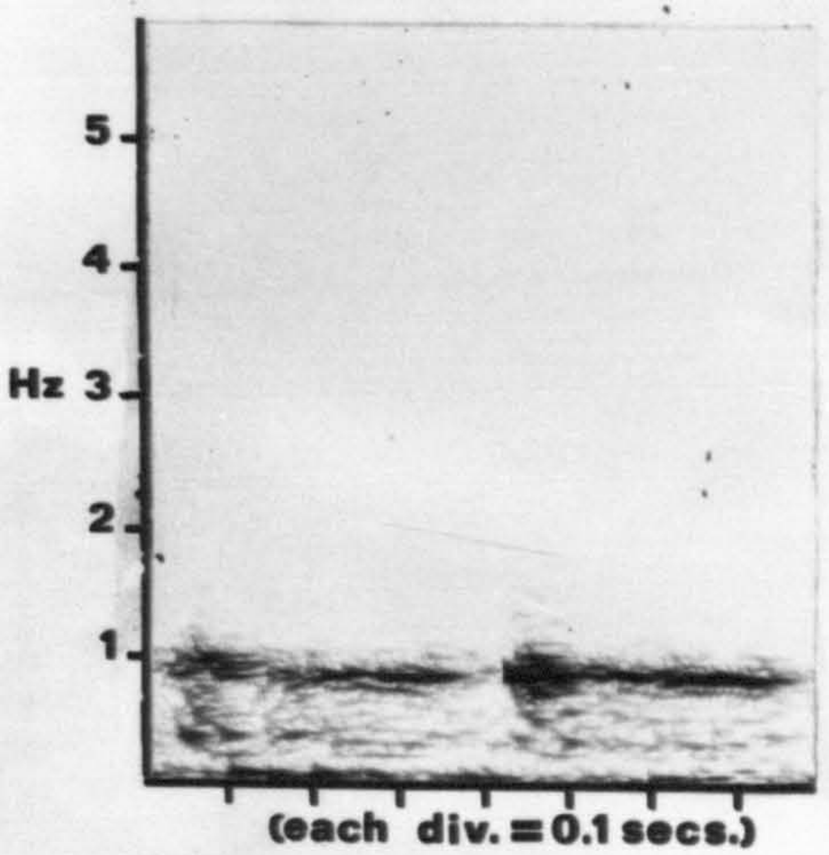


FIG. 5.1 (a) Volley call.



(b) Part of same call.

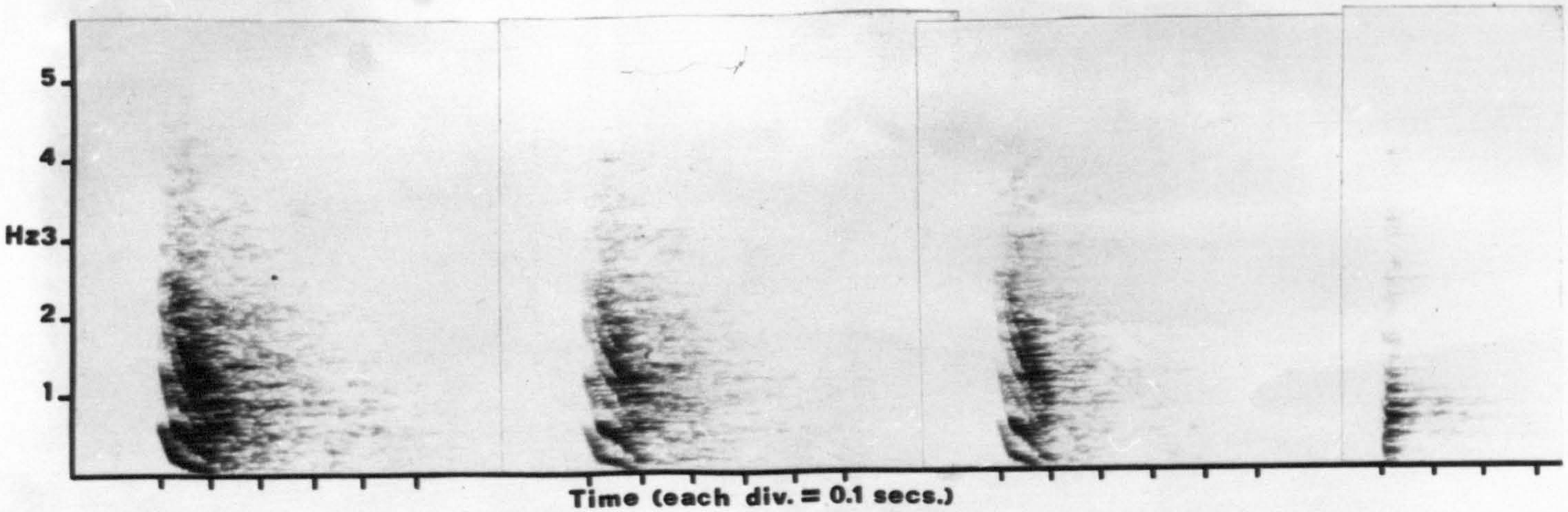


FIG. 5.3 Explosive calls, 2nd, 3rd, and 4th in series. Redtail pop.

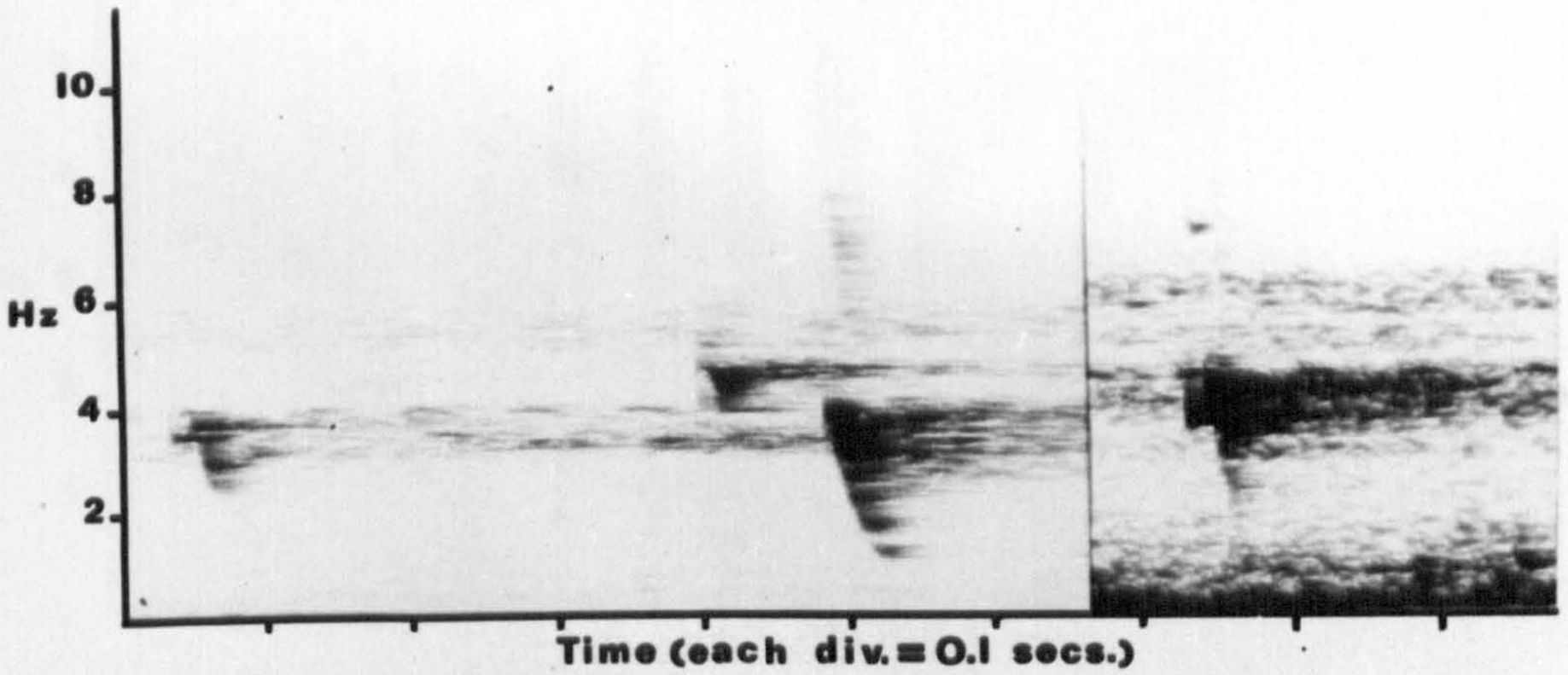
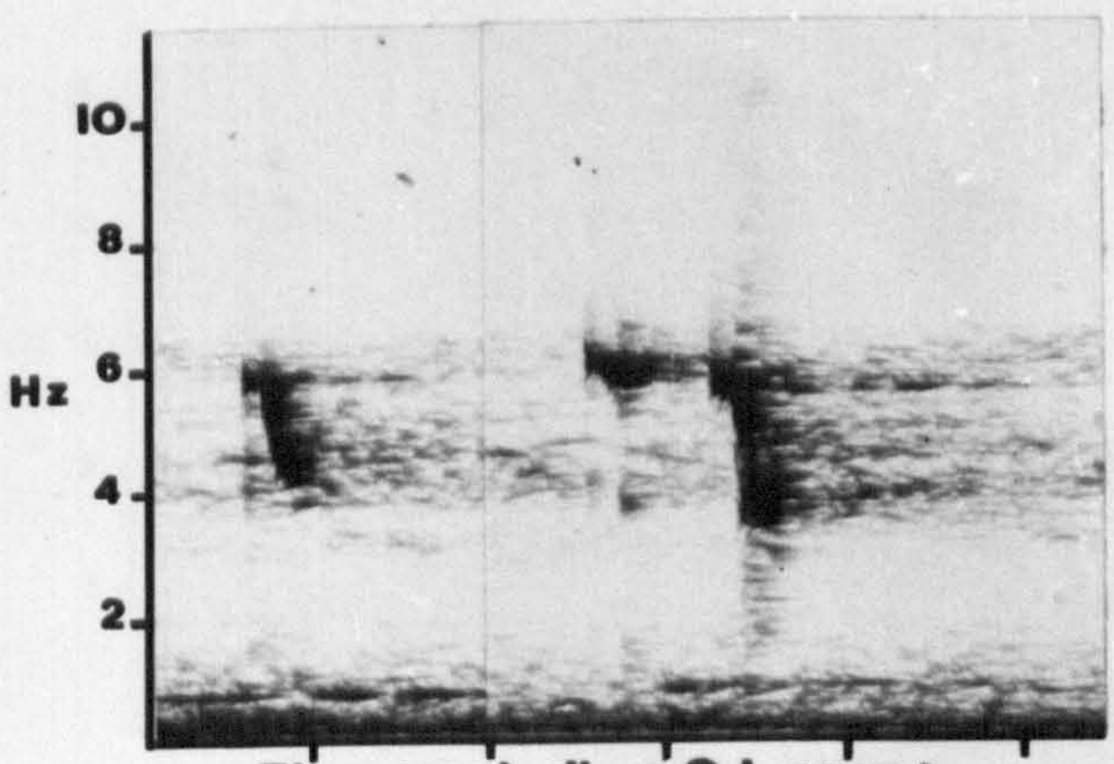


FIG. 5.5 Chirps.



Chirps (cont.)

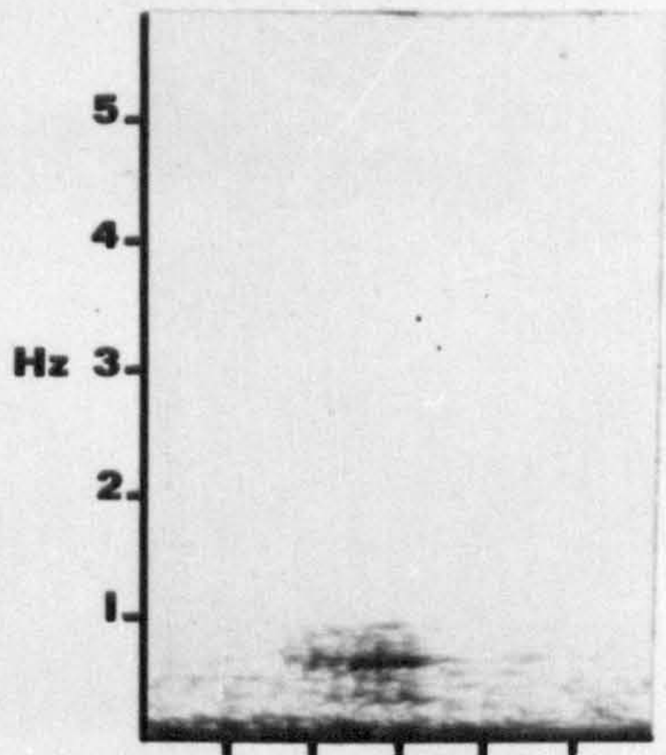


FIG. 5.6 Croak

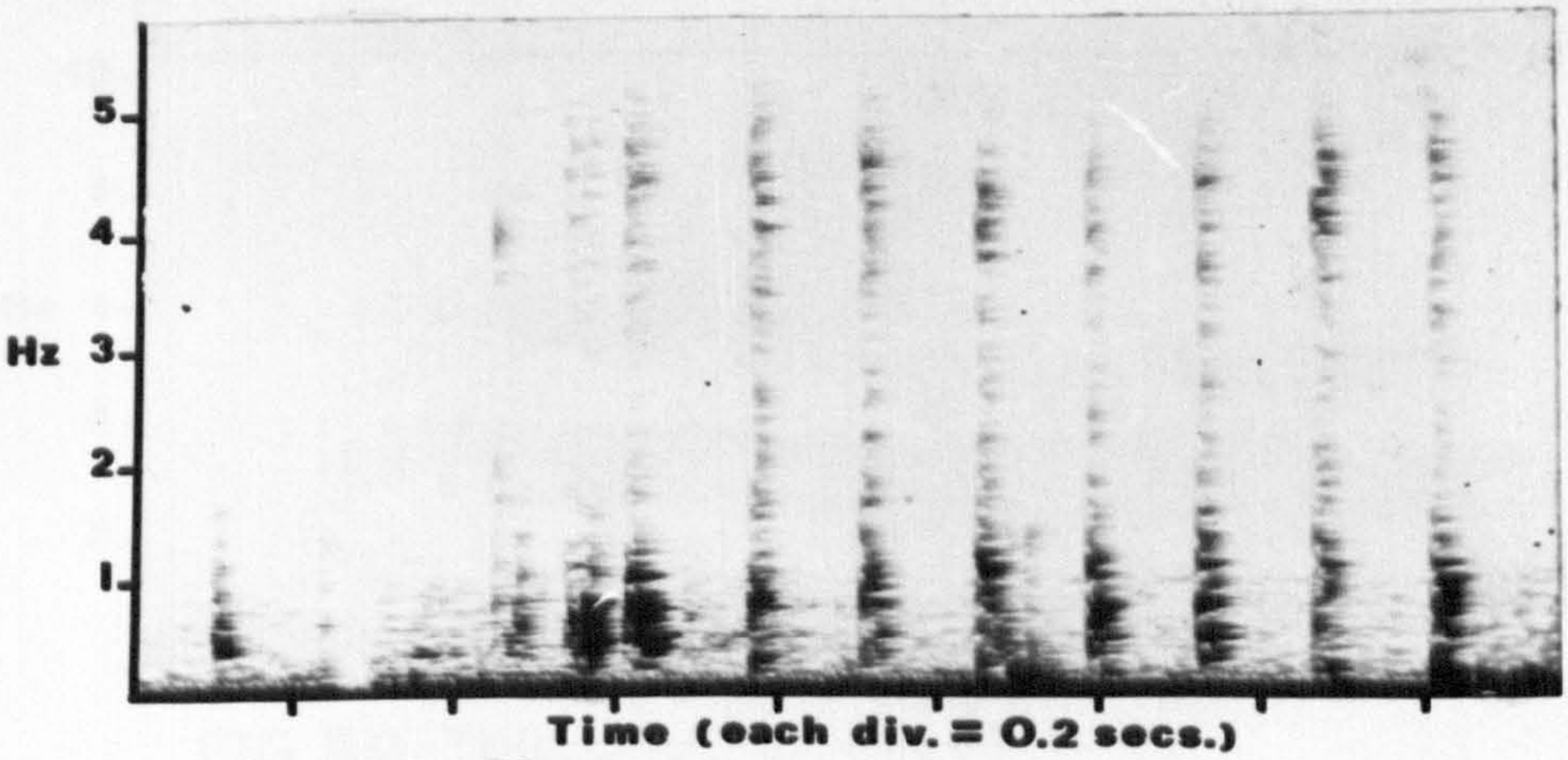


FIG. 5.7 Chatter

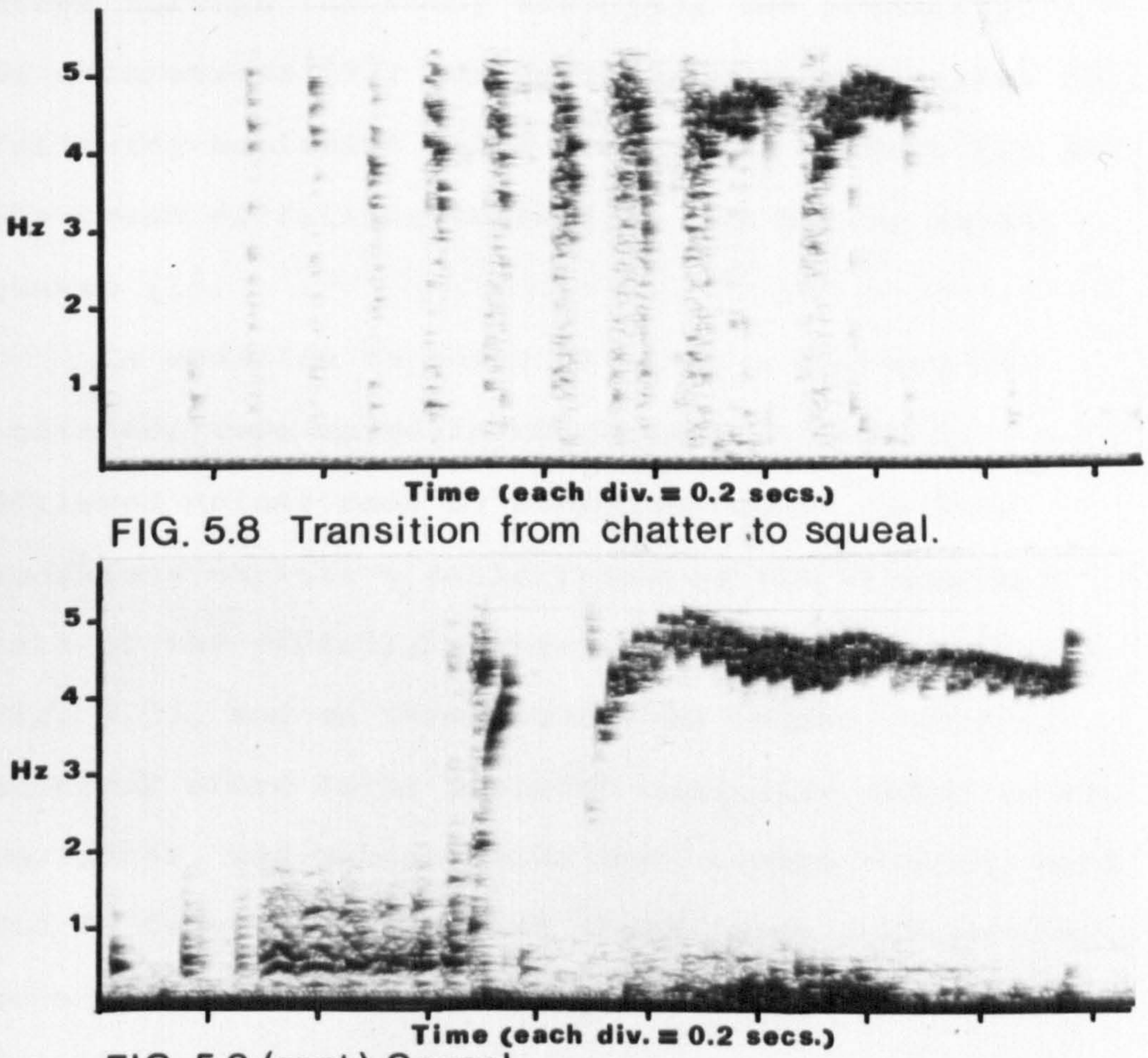


FIG. 5.8 Transition from chatter to squeal.

FIG. 5.8 (cont.) Squeal.

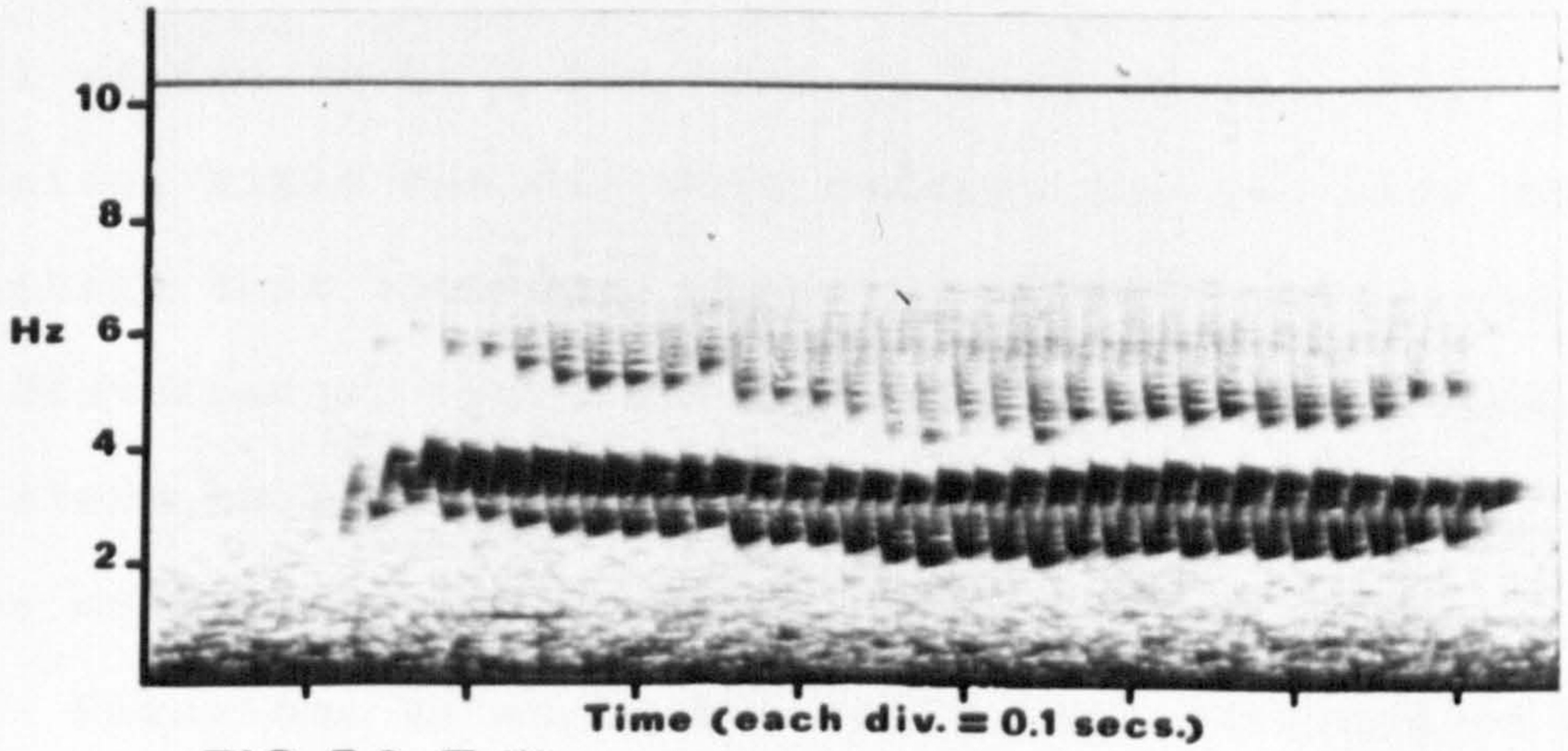


FIG. 5.9 Trill.

track through the study area (4), the proximity of chimpanzees (1), during intergroup encounters (3), following explosive calls from other monkeys (2) and the crash of falling trees (3), and during earthquakes (1).

In addition to these 51 cases a further 20 instances were noted in which explosive calls followed noises made by other animals. On five occasions explosive calls followed the equivalent call of the redtail, a quieter popping sound (see fig. 5.3), and on three occasions redtail chirps. Bushbuck alarm barks preceded explosive calls in six instances, and baboon barks and colobus roaring each did so twice. In many of these cases both species were no doubt reacting independently to the same stimulus. In some at least, though, the blue monkey call seemed to be a response to that of the other species, since the distance between the two made it unlikely that they were reacting to the same source of disturbance. For instance a bushbuck which gave an alarm bark on seeing me might be answered by a blue monkey 150 to 200 yards away, out of sight.

Reactions to explosive calls were recorded on 22 occasions. On three of these the animals being watched did not appear to respond at all. On two

others they merely looked towards the source of the noise and carried on with whatever they were doing. More typically they would exhibit behaviour interpreted as indicating mild nervousness, such as urination, scratching, or chirping (see below), but would soon resume normal activity. In one case a baby ran to its mother and clung to her following an explosive call nearby. In two instances monkeys moved slowly away from the source of the noise, but in one of these there were chimps in the vicinity so they were probably avoiding them rather than the male that made the call. Only twice did monkeys show any very marked reaction to explosive calls. An adult that was feeding in an isolated bush 75 yards out in the savanna leaped out of it and ran back into the forest immediately on hearing an explosive call, and similarly an adult feeding on the forest edge ran back into it following such a call.

Explosive calls, then, are given by mature males in a variety of situations that could be described as disturbing, but they are not strictly speaking alarm calls in the sense of being an immediate response to aversive stimuli. They could be considered as warning other members of the group of potential danger. While they can generally be traced

to some disturbance in the environment they would often provide incidental information as to the whereabouts of the mature male in each group, and so could play some role in both group cohesion and intergroup spacing.

(iii) Chirps, twitters and clicks.

Chirps are high pitched, birdlike sounds, rather variable in form. They are made by all classes apart from mature males. Commonly each chirp is made up of one or two units, but sometimes of three or four. Such multiple chirps could be described rather as twitters. Spectrograms of various types of chirp are shown in fig. 5.5. Single chirps are typically about 0.13 secs in duration (range 0.075 - 0.2 secs), and extend from about 2.6 KHz to about 4.4 KHz in frequency. In double chirps the first unit is shorter, about 0.07 secs (range 0.05 - 0.1 secs), and higher pitched, covering a frequency range of from 4.25 KHz to 5.35KHz. The second unit is longer, 0.15 secs (range 0.1 - 0.2 secs), and covers a wider range of pitch, typically from about 2.1 KHz to 5.3 KHz. Faint overtones may extend to 11 KHz. Chirps are occasionally given singly, but more commonly in bouts at intervals of a few seconds. Bouts may last for two to three minutes.

Captive monkeys were heard to make very quiet clicking noises, audible only at a distance of a few feet and hence unrecorded in the wild. No spectrograms of clicks are available, but they appear to merge into chirps and to be similar in causation; hence the two types of call are treated together.

The probable causes of chirps were determined in 95 instances. In 51 of these they were given either when contact was established with the monkeys and they first saw me, or when individuals that had been aware of my presence for some time moved up close, to within 25 yards, during the course of their activities. Often the first indication that monkeys were in the vicinity was an outburst of chirps from the obscurity of dense vegetation; only when they had thus given away their position were they seen. On 10 occasions chirps were given during aggressive incidents, either within or between groups, by monkeys not directly involved in them. In a further 10 cases chirps appeared to be given as a reaction to explosive calls, and in three cases they followed volley calls. In 7 instances monkeys chirped when other individuals moved into the same tree with them, or moved around nearby. Other circumstances in which they were given included the approach of chimpanzees

(2) or birds of prey (1), people talking nearby (2), during play (1), and following bushbuck barks (5) and the crash of falling trees (3).

In the captive group at Makerere chirps were given following sudden movements by other monkeys, particularly during aggressive incidents, people appearing near the cage, and so on. Clicks were given under circumstances similar but involving less sudden movement or novelty. A strange person, for instance, might evoke chirps whereas one well known to the monkeys might elicit only clicks.

Monkeys seldom showed any obvious, clear cut reaction to chirps. Since chirps are very much quieter than the two preceding calls it is less easy to decide whether a particular piece of behaviour does constitute a genuine reaction. Monkeys hearing chirps are relatively nearer to those making them, and hence could be responding at least in part to the same stimulus as elicited the chirps rather than to the chirps alone. For instance in 11 cases chirps were followed by explosive calls from males out of sight of the observer, but the possibility that the males had in fact seen me and were responding to my presence rather than to the chirps cannot be excluded. Twice monkeys gave croaks (see below) apparently in

response to chirps. On two occasions babies ran to their mothers and clung to them following chirps from other monkeys nearby, and once a female ran to her baby and picked it up under the same circumstances.

(iv) Croaks.

Croaks are quiet, low pitched calls, and are made by all classes. They proved very difficult to record; a spectrogram is shown in fig. 5.6, but may not indicate the full frequency range of the call. The duration is about 0.2 secs, and most of the energy appears to be at a lower frequency than in the previous calls, between 0.25 and 0.7 KHz.

The circumstances preceding the emission of croaks were established in 47 cases. In 34 of these they appeared to be made in response to the sight of other monkeys moving nearby. For example if a party of monkeys were feeding and others moved into the same tree their arrival would generally be marked by croaks. On a further 6 occasions croaks were given when parties of monkeys that had been inactive for a long period started to move about again. Of the remaining 7 instances croaks were given following explosive calls in four, volley calls in one, and the appearance of the observer in two cases.

The usual reaction to croaks was for other

monkeys to answer with croaks themselves. Thus in 15 of the 17 cases in which reactions to croaks were recorded other monkeys responded likewise. In the remaining two they merely looked towards the source of the calls, but did not answer.

Marler (1968) classifies certain signals as serving to maintain spacing within groups. He gives as an example the 'progression grunt' of vervets (Struhsaker 1967d), which apparently helps to hold the group together, and continues ' ... Two other species of Cercopithecus, C.ascanius and C.mitis, have similar calls, also contagious, given in this context, and again they seem to function by enabling foraging animals to maintain a certain distance between them'. Assuming, as seems probable, that the same call is being referred to, this interpretation could perhaps be questioned. Exchanges of croaks were commonly heard from parties of active monkeys, but careful observation indicated that calls were not as a rule exchanged by monkeys that were out of sight of one another. Only when visual contact had been established did one monkey croak, whereupon others might answer. Thus croaks were usually exchanged over fairly short distances, in the order of 10 to 30 yards. Once a monkey was seen to move

towards another, from a distance of 80 yards, after an exchange of croaks, but as a rule these exchanges did not appear to have any obvious effects on the movements of the animals concerned. Hence although croaks would provide incidental information about the location of the animals giving them, as indeed would other types of call, the maintenance of contact between individuals would not appear to be their normal function. As we have already seen, the blue monkey group is characterised by a notable lack of coherence and rigid individual spacing.

(v) Grating calls.

These are short, harsh, jarring noises, higher pitched than croaks, and sounding as if they are made up of three separate units. Unfortunately it did not prove possible to record any for spectrographic analysis. Members of all classes were heard to give such calls.

The situations in which grating calls were made were recorded in 22 instances. In 17 of these the calls were given during aggressive incidents (9 intergroup and 8 intragroup) by monkeys that were chasing or threatening other individuals. In a further two cases monkeys not involved in actual chases themselves during intergroup encounters gave

grating calls during chases by other individuals. In the remaining three instances grating calls were made by blue monkeys that were chasing or threatening redtails. On a further 10 occasions grating calls were heard to emanate from violent disturbances in the foliage, and it seems reasonable to assume that they also were agonistic. Thus unlike the calls already considered grating calls are confined to a highly specific situation; such lack of ambiguity in calls involved in aggression might be expected on evolutionary grounds.

Reactions to grating calls were seldom clear cut; as a rule it was impossible to tell whether other monkeys were reacting to the situation as a whole ... the sight of other animals chasing one another, and other noises ... or just to the one type of call. On 6 occasions other monkeys some distance from the disturbance looked towards the source of noise, and on two further occasions not only looked towards it but moved off in that direction. In two other instances monkeys ceased grooming or 'started' suddenly on hearing grating calls at a distance of 100 yards. Grating calls were followed by explosive calls three times and by volley calls once, but these were more likely to be reactions to the overall situation than to grating calls <u>per se</u>.

(vi) Chatters and squeals.

Chatters are bursts of noise made up of a series of distinct units; the call could be rendered as 'chi-chi-chi-chi-chi-chi- ... '. All classes other than mature males were recorded as making chatters. Spectrograms of chatters are shown in fig. 5.7. The individual columns of noise are generally 0.05 - 0.075 secs. in duration, and are given at a rate of one every 0.10 - 0.15 secs. Each unit covers a wide range of frequencies. In a low intensity chatter there is a tendency for some concentration of energy in the lower frequencies, but in the more intense versions greater emphasis is found in the higher frequencies and the call sounds more shrill. At very high intensity the high frequency elements are further exaggerated and fuse into a continuous squeal. This transition is illustrated in fig. 5.8.

The circumstances under which chatters were given were determined on 20 occasions. In all but one of these they were given during agonistic incidents (14 intragroup and 5 intergroup) by monkeys that were being chased or attacked. In the remaining instance the call followed the appearance of a bird of prey. On a further 6 occasions chatters were heard coming from violent disturbances in the foliage;

no details could be seen, but once again it seems reasonable to assume that the interactions involved were agonistic in nature. Similarly in the 7 instances in which monkeys making squeals were identified all were individuals being chased or attacked.

As with grating calls, reactions to chatters could seldom be distinguished from reactions to the situation as a whole. The most typical response was again for other monkeys to stop whatever they were doing and look towards the source of the noise.

(vii) Trills.

Trills are high pitched, bird-like calls, given by all classes other than mature males. A spectrogram is shown in fig. 5.9, but the recording is of poor quality and may not give the whole range of frequency.

The situations in which trills were made were recorded in 11 cases. In 6 of these they were given by monkeys when others moved into the same tree as them or moved towards them from nearby. Once a trill was given by a juvenile, standing at the end of a thin branch, as a mature male walked up to within a few feet of it. Twice trills were made by playing

infants, one wrestling with another infant and the other with an adult. In the remaining two instances trills were given following the appearance of the observer and after the crash of a falling tree.

In the captive group of C.albogularis at Makerere two infant males often gave trills if the mature male approached them, and trills were also given following the appearance of people with food.

Reactions to trills were seldom clear cut. In three instances trills were followed by croaks, but these could have been responses to the sight of other monkeys moving rather than to the trills as such.

(viii) Screams.

This call, superficially similar to a squeal but much louder and quite distinct, was heard only once. A violent disturbance in the foliage was followed by an outburst of shrill screams, like the cry of a wounded hare. A male and another adult emerged from the source of the disturbance. This adult appeared to have blood on its perineal region. It stood looking up at the male, with tail vertical, and then ran off. If one might be permitted a temporary lapse into anthropomorphism, it could be suggested that this represented a frustrated (or maybe successful) attempt at rape. Struhsaker (1967d) describes an

'anti-copulator-squeal-scream' made by adult and sub-adult nonoestrous female C.aethiops when males attempted to copulate with them, so this call may be comparable.

Other noises.

In a study of communication in the various primates of Budongo Marler (pers.comm.) classified blue monkey calls into categories closely resembling those above, but recorded in addition a deep 'boom', made only by adult males. I also heard what was probably the same noise, but thought at the time that it was made by chimpanzees, not by blue monkeys. This well illustrates, incidentally, the problems of studying communication in thick forest; if a noise is uncommon one may not even discover what makes it, let alone its significance. In the few instances in which booms were recorded in my notes they generally followed the crash of falling trees. In some cases there were definitely chimps in the vicinity. In one instance a boom was made during an intergroup encounter. Apparently after I left Makerere the mature C.albogularis male in the captive group there started to make a similar noise, given after social disturbances in his own group or a group of vervets in an adjoining cage (Rowell, pers.comm.).

In addition to the calls described above blue monkeys make a variety of coughing and sneezing sounds, but these appear to be nothing more than coughs and sneezes and to have no communicatory function.

COMPARISON WITH OTHER SPECIES.

Marler (1965) suggests that repertoires ranging in size from about 10 to about 15 basic sound signal types may be characteristic of non-human primates as a whole. The repertoire of the blue monkey falls at the lower end of this range. However comparison of the numbers of calls made may not be the best method of contrasting the vocal repertoires of different species. In some calls are highly stereotyped, whereas in others they may be very variable. For example Rowell and Hinde (1962) describe how certain rhesus monkey calls merge into one another with all degrees of intermediate. Likewise chimpanzee calls may form such a graded series (Reynolds and Reynolds 1965, Van Lawick-Goodall 1969, Marler 1969b). Any division of such a series into discrete units must be to some extent arbitrary and merely a matter of descriptive convenience. Most blue monkey calls appear fairly stereotyped, but some, such as chirps, are rather variable, and chatters and squeals form a graded series.

Little information is available on the repertoire of other Cercopithecus spp. Andrew (1963) classifies Cercopithecus calls into five broad categories, but the relation between these and the present scheme of classification is not always clear and some calls are not mentioned at all. The calls of vervet monkeys in the wild have been described by both Gartlan (1966) and Struhsaker (1967d). On Lolui Island Gartlan described 13 distinct calls, whereas for the Amboseli Reserve Struhsaker listed 36 physically or audibly distinct sounds (including, however, coughing, sneezing, and vomiting). Some of this contrast in the size of repertoire may be the result of differences in the criteria used to distinguish calls, but some at least appears to reflect a genuine difference between the two populations. Few of these calls have any similarity to blue monkey calls as regards structure, and even functional analogies are seldom clear cut, but this is perhaps not surprising considering the very different conditions of forest and savanna life and the effects that they must have on systems of communication.

As yet no full account of the vocal repertoire of any forest Cercopithecus sp. has been published, but certain calls of C.nictitans and C.cephus have been discussed by Gautier (1969). Like the blue

monkey both these species have two loud calls, made only by mature males and by a single male in each group. One of the calls of C.nictitans appears from spectrograms to be very similar in form to the explosive call of C.mitis, and apparently sounds much the same to the human ear (Gartlan, pers.comm.). It is given in the same circumstances; following claps of thunder, the fall of trees, calls by other monkeys, and so on. Gautier considers its function to be the location of groups and maintenance of spacing between them. The second type of call is given when two groups are in close proximity, and tends to increase the distance between bands. It is given also in response to predators, and would thus appear to be equivalent to the blue monkey volley call. As with C.mitis explosive and volley calls the two types of call are often given in association.

The calls of C.cephus are similar, but the two species are nearly always found in association and the C.cephus equivalent of the explosive call is generally given in response to the comparable C.nictitans call. It does not appear to have any effect on the spacing of neighbouring C.cephus groups, but seems to act rather as a 'rallying call' for members of the same group. Likewise the C.cephus

equivalent of the volley call is given in response to predators, but has no obvious effect on inter-group spacing. Gautier suggests that through association with C.nictitans the C.cephus calls have lost their intergroup spacing function, the louder calls of C.nictitans serving as a spacing mechanism for both species. Gartlan, working in another part of West Africa, obtained evidence suggesting that while C.nictitans was territorial, C.cephus was not (Gartlan, pers. comm.).

My own observations on C.ascanius in Budongo indicate that its vocal repertoire is basically similar to that of the blue monkey. Redtails have a call very similar to the blue monkey volley call, though it seems to be given much less often. The counterpart of the explosive call is a quieter but clearly related popping noise (see fig. 5.4), made under the same circumstances as the equivalent blue monkey call but generally singly or in short series. Redtails respond to mildly disturbing situations such as the appearance of the observer with an outburst of twitters, calls similar to blue monkey chirps but with each consisting of several units rather than the one to three characteristic of blue monkeys. Likewise redtails have a call similar in both form and function to the blue monkey croak.

We have already seen that blue monkey calls sometimes follow redtail calls; the reverse is also true. The relationship between blue monkey explosive calls and redtail pops is of particular interest. Blue monkey calls followed redtail calls on only 5 occasions, whereas redtail calls followed blue monkey calls on at least 23. Blue monkey calls were heard more often than redtail calls, though this would in part be due firstly to more time being spent watching blue monkeys than redtails and secondly to the redtail call being quieter. A possible implication, however, is that the redtail sometimes responds primarily to the blue monkey call rather than to disturbances in the environment per se. One is tempted to draw an analogy with the relationship between C.nictitans and C.cephus, but this might not withstand critical scrutiny since blues and redtails are found in association much less often (see Chapter 8).

The degree of reliance on vocal as opposed to visual signals might be expected to vary from one habitat to another (Marler 1965, Gartlan and Brain 1968). Since visibility in forest is restricted, monkeys living in such a habitat must rely to a large extent on vocal signals, particularly for long range communication. In open country, on the other hand,

conditions would favour a greater emphasis on visual signals. Visual signals differ from vocal signals in being much more directional; a call might be heard by all members of the group, and perhaps by predators as well, whereas a facial expression might be seen only by a single individual. Increased reliance on visual communication would hence both minimise the risk of detection by predators and facilitate the development of complex social relationships within the group.

Increased emphasis on visual communication in open country species could be manifested by an increase in the repertoire of such signals, by a reduction in their degree of stereotypy, by an increase in their frequency relative to vocal signals, or by any combination of these. To determine whether open country species do in fact rely more on visual signals is hence far from straightforward. Comparison of the repertoires of different species may be further complicated by taxonomic considerations. Contrasts between distantly related taxa will be less closely allied to differences in habitat than will contrasts between closely related species.

The most meaningful comparison in the present case is that between C.mitis and C.aethiops. As

Gartlan and Brain (1968) point out, the facial musculature of C.mitis is less mobile than that of C.aethiops, and C.mitis lacks contrasting colouration such as white eye patches to accentuate facial expressions. My own observations on C.mitis suggest that its repertoire of postures also is less than that of C.aethiops, (see, for example, p. 314). On the other hand the vocal repertoire is smaller too, so it is difficult to say whether the emphasis on vocal communication is relatively greater. Relative size of vocal and visual repertoires within a species is anyway no reliable indication of the amount each is used. Chalmers (1968c), for example, described four visual displays and five types of call in the black mangabey, but saw 3.75 times as many vocal as visual signals given. No comparable information is available for the two Cercopithecus spp.

Chapter 6

SOCIAL BEHAVIOUR II

METHODS OF ANALYSIS.

In forthcoming sections data will be presented on the frequency of various types of interaction between the different sex and age classes. If such figures are to give an insight into social structure, they must be compared with expected values based on the assumption that all individuals interact randomly with other members of the group. The calculation of these expected values poses a variety of problems. The approach to be developed is similar in principle to those of Altmann (1968) and Chalmers (1967, 1968b), but differs in several respects.

Firstly, it has to be decided which set of group compositions to use as a basis for calculation. The March 1967 figures for groups A,B,C, and D have been employed throughout, since they are considered more accurate than the September 1966 figures and all but a fraction of the data was collected from these four groups rather than from groups E and F. It will be noted, however, that differences between the two sets of compositions are only marginal.

Use of a particular set of compositions makes no allowance for changes, resulting either from birth and growth of individuals or from mortality or possibly movement of monkeys from one group to another,

during the course of the study. For instance Struhsaker (1967a) in his study of C.aethiops makes use of 'weighted mean group sizes', calculated by multiplying the size of the group by the estimated number of days that the group remained that size, summing these products, and then dividing this sum by the total number of observation days. Weighted compositions could be obtained in the same way. Altmann (1968), for example, calculated expected values from relative numbers of 'monkey years of availability' for the various classes, rather than from actual numbers in censuses at any one moment. In the blue monkey, though, observational conditions preclude the accurate recording of such changes as may take place. It has therefore to be assumed that any variation in composition is insufficient to render the counts used unrepresentative.

Secondly, it was frequently not clear which group was being observed. The data cannot therefore be split up among the groups from which it originated, but has rather to be considered as a whole. Since the amounts of data for many types of interaction are small, information from all groups would anyway have to be combined to give a large enough sample for statistical analysis. Were there little variation in

composition from one group to another and observations spread fairly evenly over the groups, calculations could be based on a 'mean group composition', i.e:

MM	YM	F	UA	J	I	B	T	*
1.25	0.75	4.75	1.25	2.25	3.0	1.0	14.25	

While observations probably were spread fairly evenly over the four groups, differences in group composition, though small, are perhaps sufficient to introduce minor distortions when interactions between two animals of determinate class are considered. An alternative approach, which overcomes this difficulty, is to calculate probabilities of interaction for each group individually, and to employ the means of these individual group probabilities. This again involves the assumption that amounts of observation on each group were roughly equal, but gives a more accurate assessment of probabilities, particularly for classes such as mature males and babies. The latter approach has therefore been adopted.

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* The following abbreviations are used in this and succeeding tables: MM .. mature males, YM .. young males, F .. females, UA .. unsexed adults, A-M .. adults other than mature males, J .. juveniles, I .. infants, B .. babies, T .. total.

A further problem is raised by the unsexed adults in three of the four groups. These cannot be treated as a separate category when calculating expected values, since the chances of an adult being unsexed in the group compositions almost certainly differ from its chances of being unsexed during observation of a particular interaction. Unsexed adults would be either young males or females, probably nulliparous; mature males are distinct by virtue of their greater size. They could be allocated to these two categories in the same proportions as identified females and young males, but this would probably produce a bias towards females. In practice the chances of an adult unsexed in group compositions belonging to either class are probably about equal; half have therefore been considered as females and half as young males. Adjusted to take account of this the group compositions become:

	MM	YM	F	J	I	B	T
A	2	1	6	3	3	-	15
B	1	1.5	5.5	2	3	1	14
C	1	1.5	5.5	2	3	2	15
D	1	1.5	4.5	2	3	1	13

The probability of an animal of a particular class performing any item of behaviour will be equal to the proportion that that class constitutes of the

group total. For example, for mature males in group A the probability would be $\frac{2}{15}$, i.e. 0.133. Probabilities for each class in the population as a whole are as follows:

MM	YM	F	J	I	B	T
0.088	0.096	0.377	0.158	0.211	0.070	1.0

These probabilities apply to acts involving one animal only, or to one participant in a dyadic interaction in which the other participant is of unspecified class. For instance the probability of an animal seen standing on its head being a mature male would be 0.088. Likewise, and more credibly, mature males might be expected to initiate 8.8% of all grooming interactions, or to be the aggressor in 8.8% of all aggressive interactions.

For estimating expected numbers of dyadic interactions a different set of probabilities have to be used. These are calculated on the basis of sampling without replacement. Suppose, for example, one wanted to calculate the chances of an interaction in group A involving two females. The chances of one animal being a female would be $\frac{6}{15}$. The chances of a second animal from those remaining also being female would be $\frac{6 - 1}{15 - 1}$. Hence the probability of a female/female interaction would be $\frac{6}{15} \times \frac{5}{14}$, i.e. 0.1428.

A general formula for calculating the probability of interactions between members of a like class would be $\frac{x}{T}\left(\frac{x - 1}{T - 1}\right)$, where x is the number of animals of that class and T the total number of animals in the group.

For animals of unlike class the formula must be modified. Suppose one wished to calculate the probability of mature male/female interactions in group A. The chances of one animal being a mature male would be $\frac{2}{15}$. The chances of a second animal from those remaining being female would be $\frac{6}{15 - 1}$. Thus the chances of a male initiating an interaction with a female would be $\frac{2}{15} \times \frac{6}{15 - 1}$. Conversely the chances of a female initiating an interaction with a male would be $\frac{6}{15} \times \frac{2}{15 - 1}$, which is exactly the same. Hence the probability of mature male/female interactions, irrespective of which class initiates them, would be $\frac{2 \times 6 \times 2}{15 \times 14}$, i.e. 0.1142. A general formula for calculating the probability of interactions between unlike classes would be $\frac{2xy}{T(T - 1)}$, where x and y are numbers of animals of the two classes in the group, and T the group total.

Probabilities for all possible types of dyadic interaction within each group were computed. Means of the individual group probabilities were then

calculated to give the values to be used in the analysis of the data. These probabilities are shown in fig. 6.1. Marginal totals give the overall probability of a particular class being involved in an interaction. Note that these are different to the proportions of the various classes in the population as a whole. For instance females constitute 37.7% of the population, and would therefore be expected to <u>initiate</u> 37.7% of all interactions, but to <u>participate</u> in 62.8%.

In many instances we wish to know the probability of one member of a dyad initiating the interaction, or playing some particular part in it. For instance we might want to determine an expected value for mature males grooming females, as opposed to participating in grooming interactions with them. It will be clear from the calculations above that the chances of an animal of one class <u>directing</u> a particular action to an animal of another class is half the probability of an interaction <u>involving</u> the two classes. For interactions between members of like classes, on the other hand, the probability of one directing an action to another is the same as the probability of them participating in an interaction together. These probabilities are given in fig. 6.2.

Note that the marginal totals in fig. 6.2 are effectively the same as the probabilities on p.214 .

Using the probabilities in figs. 6.1 and 6.2 we may determine whether interactions in the group as a whole are non-random, but not, strictly speaking, whether members of any one class interact at random with all other classes. To establish whether the latter is the case a further set of probabilities must be calculated.

Suppose, for example, one had found that females in group A participated in a particular type of interaction, or directed some action to other monkeys, 100 times. What proportion of this total would one expect to be female/female interactions? The chances of an animal from those remaining in the group being female also would be $\frac{6 - 1}{15 - 1}$, i.e. 0.3571. Thus one would expect 36 of these 100 interactions to be female/female interactions. Likewise the chances of another animal being a mature male would be $\frac{2}{15 - 1}$, i.e. 0.1428, and hence one would expect 14 of the 100 interactions to be mature male/female interactions. General formulae for calculating the probability of interactions given that one participant is of known class are as follows:

For members of the same class, $\frac{x - 1}{T - 1}$, where x

is the number of that class in the group, and for members of another class, $\frac{y}{T-1}$, where y is the number of that class in the group, and T the group total in each case.

Probabilities were computed for each group separately on this basis, and the means of the individual group probabilities calculated. These are shown in fig. 6.3. Note that they differ from both the sets of probabilities already given. Considerable care has to be exercised to ensure that the appropriate probabilities are used in the various stages of the analysis.

As a rule the first step is to determine whether the number of interactions in which the various classes participate could be predicted from the group compositions. For this purpose the probabilities in fig. 6.1 are used. If, on the other hand, we are concerned with actions, such as grooming or being groomed, rather than with participation in interactions, the probabilities in fig. 6.2 are employed. The second step is to take each class individually and see whether its partners in interactions are drawn from all classes at random, irrespective of whether it participates in more or fewer interactions than would be expected from the

FIG.6.I Probabilities of dyadic interactions between the various age-sex classes.

	mature male	young male	female	juvenile	infant	baby	TOTAL
mature male	0.0023	0.0172	0.0711	0.0309	0.0392	0.0106	0.1713
young male	0.0172	0.0031	0.0781	0.0320	0.0445	0.0160	0.1909
female	0.0711	0.0781	0.1243	0.1280	0.1707	0.0556	0.6278
juvenile	0.0309	0.0320	0.1280	0.0154	0.0714	0.0213	0.2990
infant	0.0392	0.0445	0.1707	0.0714	0.0320	0.0321	0.3899
baby	0.0106	0.0160	0.0556	0.0213	0.0321	0.0095	0.1451

FIG.6.2 Probabilities of the various classes directing actions to one another.

	mature male	young male	female	juvenile	infant	baby	TOTAL
mature male	0.0023	0.0086	0.0356	0.0155	0.0196	0.0053	0.0869
young male	0.0086	0.0031	0.0391	0.0160	0.0223	0.0080	0.0971
female	0.0356	0.0391	0.1243	0.0640	0.0854	0.0278	0.3762
juvenile	0.0155	0.0160	0.0640	0.0154	0.0357	0.0107	0.1573
infant	0.0196	0.0223	0.0854	0.0357	0.0320	0.0161	0.2111
baby	0.0053	0.0080	0.0278	0.0107	0.0161	0.0095	0.0774

FIG.6.3

Probabilities of dyadic interactions given that one participant is of known class.

Known class:	mature male	young male	female	juvenile	infant	baby	TOTAL
mature male	0.0178	0.1047	0.4048	0.1693	0.2272	0.0757	I.0
young male	0.0936	0.0289	0.4048	0.1693	0.2272	0.0757	I.0
female	0.0936	0.1047	0.3290	0.1693	0.2272	0.0757	I.0
juvenile	0.0936	0.1047	0.4048	0.0936	0.2272	0.0757	I.0
infant	0.0936	0.1047	0.4048	0.1693	0.1515	0.0757	I.0
baby	0.0772	0.1158	0.3969	0.1544	0.2316	0.0238	I.0

group compositions. Here the expected values are calculated from the probabilities in fig. 6.3.

Yet further problems arise when one attempts to apply these methods to the data obtained. It was not always possible to classify both the individuals involved in an interaction; in many cases one or both were identified no further than being adults other than mature males. How are these cases to be treated?

One possibility would be to split them arbitrarily between young males and females, but this has obvious shortcomings. Other classes may interact preferentially with either females or young males, so allocation to one or the other category would be likely to distort the true situation.

Another possibility would be to ignore them altogether and include in the analysis only those dyads in which both participants were fully identified. This approach is superficially attractive, and may be valid when the numbers of unidentified animals are small relative to the expected numbers of females and young males. Consider, however, a hypothetical situation in which observed numbers of interactions involving either young males or females or both fall short of the

expected values by an amount similar to the number of interactions involving unsexed adults. Even though statistical treatment might show the difference to be significant, this would not necessarily prove that the shortfall was the result of non-random interaction. It could equally be due to young males and/or females not being identified in all the interactions in which they participated. The only way to get round this is to combine the observed values for young males, females, and unsexed adults, and compare them with the combined expectations for young males and females. One can then make valid statements as to whether adults as a whole, excluding mature males, behave as expected, but loses the ability to discriminate between the behaviour of young males or females. Of course difficulties of this nature only arise when the proportion of unsexed adults is large, and the observed values for females and young males are similar to or significantly below the expected values. If either of the observed values are significantly higher than expectation, then adding data on unsexed adults to them will only make them more significant. Thus the extent of the conclusions that can be drawn regarding the behaviour of females and young males will vary from one situation

to another, depending on the relation between observed and expected values and the numbers of records of unsexed adults. This should become clear when specific cases are considered.

Yet further difficulties can be raised. It can be argued that the various sex and age classes might differ in their relative visibility to the observer, and hence that the behaviour recorded could be a biased sample. For instance Chalmers (1967, 1968b) showed this to be true of the mangabeys that he studied, by noting the numbers of each class visible in half hourly censuses and comparing total sightings of the classes with their numbers in the group. Adult males were seen more often than would be expected from their proportion in the group total, and females, subadults, and juveniles less often. When comparing the frequencies of behaviour patterns shown by the different classes Chalmers calculated expected values from the relative visibility of the classes to the observer, rather than from the known number of individuals of each class within the group.

Unfortunately the validity of such an approach can be questioned. It is possible that contrasts in visibility may result in part from differences in behaviour; as Chalmers himself points out, some

types of activity are more likely to attract the observer's attention than others. Suppose, for instance, a particular class indulged in a disproportionate amount of some conspicuous activity such as aggressive chasing or territorial display. This would increase its relative visibility, but it would be misleading to use the resultant figures to estimate expected values when considering a sedentary activity such as mutual grooming. Data such as Chalmers presents show that expected values for interactions <u>seen</u> would be inaccurate if based on group compositions, but calculation of expected values from the relative visibility of the classes will not necessarily correct such errors. Only if it could be shown that behaviour patterns do not differ in their conspicuousness and contrasts in visibility are the result wholly of differences in size or appearance would estimation of expected values in this manner be valid.

In the present study insufficient data was collected in such a way as to allow reliable estimates of relative visibility. However it is considered that if such differences exist in the blue monkey they are probably not great enough to invalidate comparisons based on group composition.

Some classes might well be more conspicuous than others during the initial few minutes of an encounter, but once the monkeys had been watched for a short while and the majority of those in the immediate vicinity identified differences in visibility would be less marked. The only category that may be exceptional in this respect is females with babies; such females were noticeably more shy than other monkeys.

The possibility of differential visibility of patterns of behaviour raises further problems apart from those mentioned above. If such contrasts in visibility do exist, behaviour recorded by the observer will be a biased sample of the total behaviour of the animals. This may lead to erroneous conclusions about the pattern of organisation within the group. The problem becomes acute when one attempts to compare relative frequencies of behaviour patterns between species, particularly ones living in different habitats. Suppose, for instance, that in a forest species one had recorded five times as many friendly as aggressive interactions, and in an open country species ten times as many. This contrast could be the result either of a genuine dissimilarity in

behaviour or of differences in the relative visibility of activities under forest conditions. Aggressive chasing, for instance, might be more conspicuous than mutual grooming.

Chalmers attempted to devise means of counteracting such bias. In his half hourly censuses he noted not only the sex and age class and activity of those monkeys visible but also whether they were in full view or partially concealed by foliage and branches. It was found that the ratio of 'exposed' to 'partially concealed' monkeys was greater for moving animals than for ones engaged in sedentary activities, 4.2:1 as opposed to 2.6:1. From this it was calculated that a monkey that was not moving had only 0.89 of the chance of being exposed as one that was moving. When comparing the frequency of different activities a 'correction factor' of 0.89 was employed.

The validity of this factor can likewise be questioned. The method of calculation takes no account of the monkeys that are not seen at all, and it is these, not the ones that <u>are</u> seen even though partially obscured, that distort the results. The factor would only be valid if the ratios of 'seen' to 'unseen' monkeys for each activity bore the same relation to one another as the ratios of 'exposed' to

'partially obscured' monkeys among those that were seen. The figures quoted above certainly imply that some sedentary monkeys are being overlooked, but they do not tell one how many.

In summary, then, caution must be exercised in interpreting the numerical data that follow. A variety of assumptions have had to be made in the calculation of expected values, and the observed values may be subject to bias. If statistically significant discrepancies between observed and expected values are found, they could be the result either of genuinely non-random behaviour on the part of the animals or of distortions arising from one of both of the above factors.

How then are the figures to be construed? In some cases one can predict the direction of possible distortions. (See, for example, p.305). If in such cases the observed values depart from the expected values in the direction one would predict, little weight can be placed on the discrepancy even if it is statistically significant. If on the other hand the departure from expectancy is in the opposite direction, a statistically significant result could more safely be taken at face value. In most cases, though, one can predict neither the direction nor the

magnitude of any distortion, and hence has no option but to make a qualitative judgement as to the validity of the statistical conclusions. As a general rule statistically significant departures from expectancy will be regarded as valid indications of non-random behaviour on the part of the animals only if probabilities are less than 0.001. Lower levels of significance will be regarded only as indicative of possible trends, and any conclusions drawn from them should be tentative.

This may be considered an unsatisfactory approach, but the extent to which biased data is improved by the application of dubious correction factors is debatable. Until means of quantifying possible biases in the collection of data have been devised, if indeed they can be devised, it seems safer to present the raw data and merely to draw attention to the possibility of distortions. Certainly this is a problem that has received too little attention from primate workers in the past; with the creditable exception of Chalmers few authors have even recognised the possibility of biases, let alone attempted to correct them. Admittedly such problems are more acute in forest species than in the more intensively studied open country animals, but even in the latter

the same considerations may apply to some extent, though perhaps with insufficient force to invalidate the conclusions reached. With the literature on forest monkeys increasing rapidly, it seems important that this uncritical acceptance of observations as a representative sample of the animals' behaviour should be questioned.

GROOMING.

Introduction.

Social grooming was by far the commonest type of social interaction observed; 467 interactions involving grooming and a further 50 involving unsuccessful grooming invitations were recorded, as against only 171 for all other types of interaction combined. Information on grooming will therefore be analysed in considerable detail. A qualitative description of behaviour associated with grooming will be given first, followed by a quantitative account with appropriate statistical analysis.

Qualitative data.

Grooming may be initiated either by one animal approaching another, or between two animals that are already sitting together. As a rule one monkey solicits grooming by adopting a particular posture,

though in some cases grooming begins without any obvious invitation. These 'grooming invitations' can be grouped into six categories:

(i) The 'half crouch' position. The monkey stands with its forelimbs flexed, so that the head and front part of the body are lowered while the rump remains high. The tail is slightly arched, curving upwards for the first few inches and then down. The body is generally aligned with the long axis towards and the head facing the other animal, but sometimes at right angles to it and occasionally directly away so that the tail and anal region rather than the head and back are presented for grooming. The eyes are invariably directed downwards or away from the partner. (See fig. 6.4).

(ii) Lying. The monkey lies flat along a branch, typically dorsal side up with the arms and legs tucked in under the body but more rarely on its side or back with limbs outstretched. The body may be aligned towards or at right angles to the other animal. The face, when the monkey is lying on its front, is directed downwards, and the eyes may be closed. (See fig. 6.5).

(iii) Sitting with head low. The monkey sits facing the other animal with the back more rounded

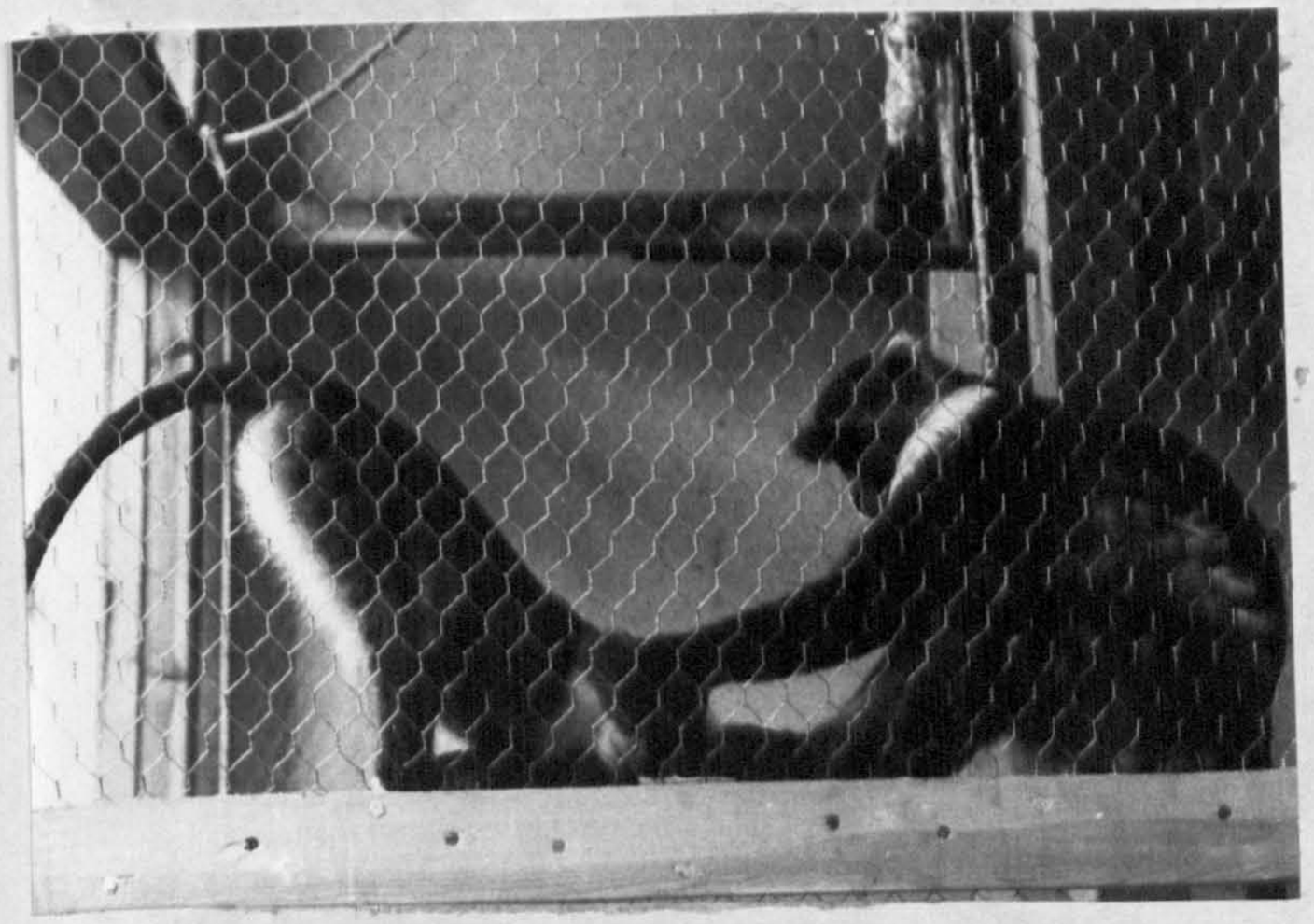
than in the normal sitting posture, and the head bent right forward so that the black crown faces the partner. (See fig. 6.6).

(iv) Sitting with head back. The animal sits upright, facing towards the other participant, with the back very straight and the head bent back or to one side exposing the pale fur on the throat and underside of the chin. One arm may be raised above the head.

(v) Standing with head low. The individual stands with the head bent forward and the tail slightly arched. The body may be aligned towards the other animal so that the black crown to the head is directed towards it, or at right angles to it.

(vi) Standing facing away. The monkey stands with the body aligned away from the other participant and the tail raised or curved forward over the back, so that the anal region is presented for grooming.

There is some variation within each of these categories, but in general the postures are well defined and there is seldom any difficulty in assigning an invitation to a particular category. In the few cases in which unusual postures were adopted they could be recognised as derivatives of more typical ones, perhaps necessitated by irregularities in the surrounding branches.



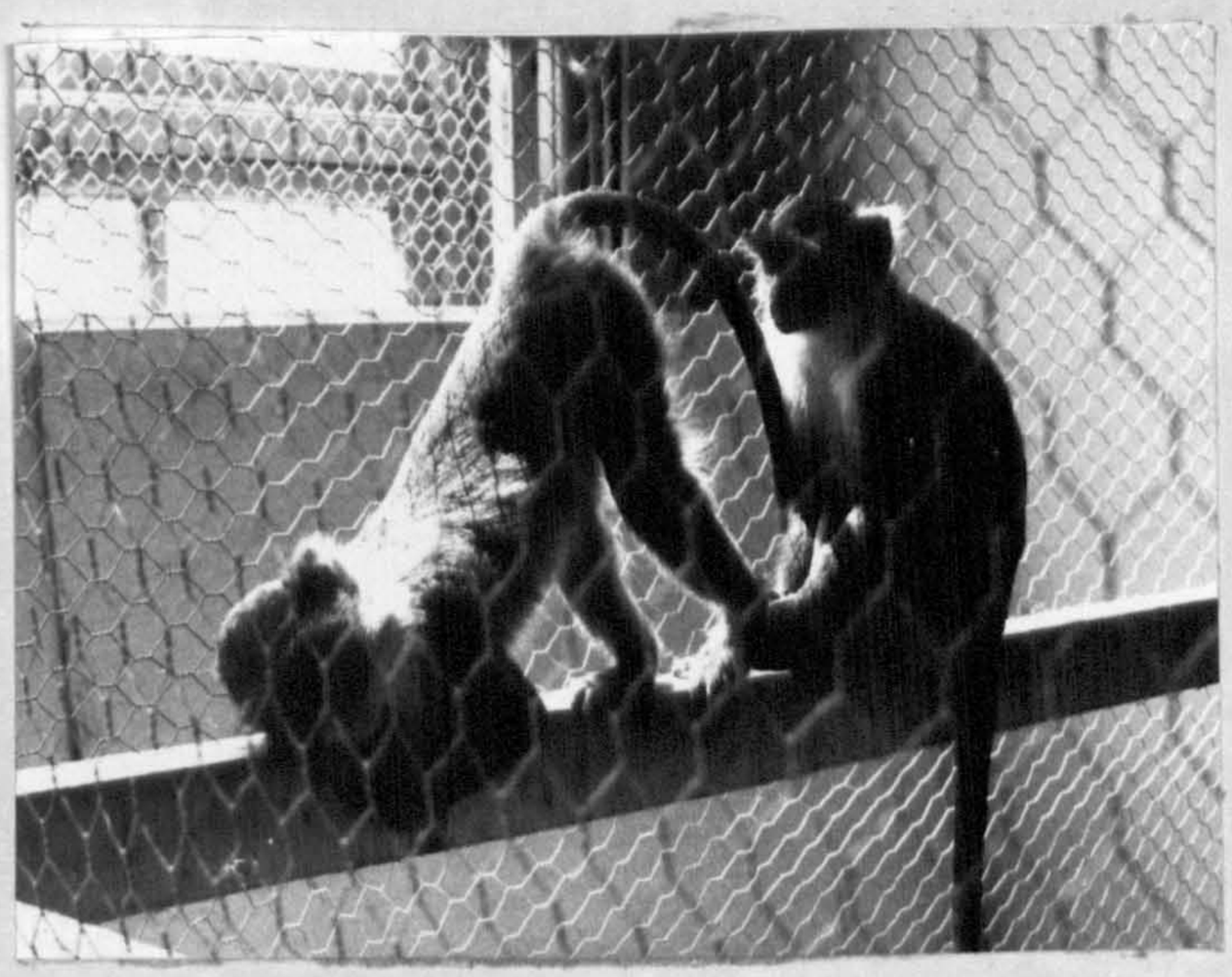


FIG.6.4 Two variants of the 'half crouch' position, as shown by captive Sykes' monkeys, C.albogularis kolbi.

FIG.6.5 One adult solicits grooming from another by lying. The latter looks away.

FIG.6.6 An adult sits with head low while another grooms it. A baby sits beside them grooming its own feet.

Some postures appear to emphasise particular features of the animals' markings, such as the black crown to the head, but this may be purely fortuitous. The only feature common to all postures is that the face is always directed away from the other participant's, visual contact being avoided; in the blue monkey as in other monkeys a direct stare is a form of threat (see below, p.311).

Similar postures for soliciting grooming are found in other Cercopithecus spp. In C.aethiops, for example, Gartlan (1966) recognises three basic postures, sitting in a relaxed position with the back straight and the chin up exposing the throat, lying, and presenting the perineal region. These clearly correspond to categories (iv), (ii) and (vi) in the present study. Positions comparable to the remaining blue monkey postures may be assumed once grooming has started. Similarly C.ascanius shows many of the same postures (pers.obs.). Parallels may be found in more distantly related species. For instance patas monkeys may solicit grooming by standing in front of another individual (Hall 1965), and baboons by lying or presenting (Hall and DeVore 1965).

Monkeys receiving grooming invitations might

respond either by facing away or turning away from the animal giving them (see fig. 6.5), or by giving a grooming invitation themselves, or by grooming.

Grooming is similar in form to the same behaviour in other species of monkey; the fur is parted and picked through with both hands, and objects removed from it either by hand or with the mouth. A contrast with C.aethiops, and with other species such as baboons, is that lipsmacking was never seen, either before or during a grooming session (cf. Gartlan 1966, Hall and DeVore 1965).

The part of the body groomed at the start of a session is related to the posture used to solicit grooming; the partner tends to groom the part of the other's body nearest to it. For instance if one animal half crouched facing towards the other the latter would groom its head or back, whereas if it stood facing away the other would groom the anal region or base of the tail. Recipients changed position frequently during the longer grooming sessions, presenting different parts of their anatomy for attention. Those parts of the body that a monkey could groom itself, such as the limbs and tail, received less attention than less accessible regions such as the head, back, and rump. This parallels findings in

other primates (e.g: chimps, Van Lawick-Goodall 1968, gorillas, Schaller 1963), and supports the view that grooming is of functional value in cleaning the fur and removing parasites in addition to having social significance (e.g: Struhsaker 1967a). Postures adopted by the recipient during grooming are similar to the soliciting postures already described, but less stereotyped.

While the majority of sessions were 'one way', some were reciprocal; one monkey groomed another and was then groomed itself. Most sessions involved only two animals, but rarely three or more might participate.

Sessions were generally terminated by the groomer stopping grooming, whereupon the participants might remain sitting together or more commonly move apart. Sometimes, though, the recipient would get up and walk away before the other partner had ceased grooming. Only rarely could the ending of a grooming session be ascribed to some disturbance in the environment, such as a tree falling or another monkey passing nearby.

<u>Quantitative data</u>.

Whenever possible the following information on grooming sessions was recorded:

(i) The sex and age class of both participants.

(ii) Whether they were sitting together at the start of the interaction, or whether one approached the other.

(iii) The type of grooming invitation, if any, adopted by the would-be recipient.

(iv) The reaction of the other individual to this invitation.

(v) Whether grooming or grooming invitations were reciprocal, and, if so, the invitation used (successfully or otherwise) by the original groomer.

(vi) The duration of the session, or of grooming by each participant in reciprocal sessions, generally to the nearest minute.

(vii) Which animal terminated the session.

(viii) Whether the participants remained sitting together or moved apart once grooming had finished.

Recording of all this information for any one session was seldom possible. For example the duration of grooming was determined in only 350 cases, and the partner terminating grooming in only 388. More importantly the sex and age class of both participants could be determined in only 250 of the 517 interactions involving grooming or grooming invitations, which leads to a variety of problems in interpreting the

data. Nevertheless enough information was obtained to provide the answers to a variety of pertinent questions. These will be considered under four headings, participation, initiation, duration, and termination of grooming.

(a) Participation in grooming sessions.

Fig. 6.7 shows the distribution of the 467 interactions in which grooming occurred among the various classes, irrespective of which groomed which or whether the sessions were reciprocal. Figures in parenthesis are expected values were association between the classes random. These are calculated as proportions of 463 (the four interactions involving totally unclassified animals being disregarded), using the probabilities in fig. 6.1. The marginal totals, therefore, give the number of occasions on which each class participated in grooming interactions irrespective of partner. At first sight the figures suggest that all classes were involved in fewer interactions than expected, but in the case of young males and females the apparent shortfall could be ascribed to the large number of unsexed adults in the sample. Young males, females, and unsexed adults have therefore to be treated as a single category. Observed and expected values for the new

category of 'adults other than mature males' are 416 and 342.9 respectively. Note that these values cannot be obtained simply by adding together the appropriate marginal totals, since this would lead to certain interactions being counted twice. It is, of course, possible that even though the new category as a whole was involved in more interactions than expected, either young males or females were involved in fewer, but there is no means of telling whether this was so.

Using the reduced number of 5 classes X^2 is calculated as 82.82 with four degrees of freedom, which is highly significant ($p = <0.001$). Hence we can conclude that the discrepancies between observed and expected values are greater than could be accounted for by chance; in particular, it appears that adults other than mature males participated in more interactions than expected, and other classes in fewer.

It may be noted that observed and expected marginal values do not add up to the same overall total. This does not mean that the expected values are wrongly calculated. Consider the hypothetical case of a group of 5 animals made up of two classes, a and b. Suppose that 2 individuals are of class a and 3 of class b. Using the formulae on p.215 we can show the probability of a/a interactions to be 0.1, of b/b interactions 0.3 and of a/b interactions 0.6. Were association random, a sample of 100 interactions would therefore be distributed as follows:

	a	b	total
a	10	60	70
b	60	30	90
			160

Class a would be expected to participate in 70 of the 100 interactions, and class b in 90. The sum of the expected marginal totals is hence 160. Now consider the following hypothetical observed distributions (expected values in brackets):

(i)

	a	b	total
a	20 (10)	60 (60)	80 (70)
b	60 (60)	20 (30)	80 (90)
			160 (160)

(ii)

	a	b	total
a	10 (10)	80 (60)	90 (70)
b	80 (60)	10 (30)	90 (90)
			180 (160)

In (i), the distribution of interactions as a whole differs from expectation, but the observed total of interactions between like classes is the same as the expected total, 40 in each case; the sums of observed and expected marginal totals are equal. In (ii), on the other hand, not only does the distribution of the observed values differ from expectation but observed and expected totals for interactions between like classes differ also, 20 as against 40; this leads to a discrepancy between the observed and expected marginal totals. It will be seen that the sum of the marginal totals can vary greatly depending on how many interactions are between members of like classes, even though the overall number of interactions is constant. If, therefore, the number of interactions between members of like classes differs from what would be expected on a random basis, the sums of observed and expected marginal totals will also differ.

92 of the 467 grooming interactions were reciprocal. Fig. 6.8 gives the number of times the various classes were involved in reciprocal sessions

with one another. The marginal totals show the number of reciprocal sessions each class was involved in, together with expected values, calculated as a pro-portion of 92 using the probabilities in fig. 6.1, were association between the classes random. X^2 is calculated as 42.67 with 4 degrees of freedom (young males, females, and unsexed adults being combined as before), for which $p =< 0.001$. Hence reciprocal sessions were not distributed randomly among the classes; in particular, adults other than mature males appear to have been involved in more than expected.

Fig. 6.9 presents the same data as fig. 6.7 broken down to show how many times each class groomed and was groomed by every other class, with expected values, from the probabilities in fig. 6.2, were grooming randomly distributed. Reciprocal sessions have been broken down into the appropriate pairs; for instance a reciprocal session between a male and a female would be scored both as a male grooming a female and as a female grooming a male. The totals for the rows show the number of times that each class groomed, and the totals for the columns the number of occasions on which each was groomed.

Comparison of the observed row totals with expected values, combining scores for young males, females and unsexed adults as before, yields a X^2

FIG.6.7 Frequency of grooming interactions between the various classes.
(Figures in brackets are expected values were association between the classes random)

	mature male	young male	female	unsexed adult	juvenile	infant	baby	other	TOTAL
mature male	-	6 (8.0)	21 (32.9)	13	6 (14.3)	5 (18.1)	- (4.9)	1	51 (79.3)
young male	6 (8.0)	-	5 (36.2)	3	2 (14.8)	1 (20.6)	- (7.4)	-	17 (88.4)
female	21 (32.9)	5 (36.2)	34	59	28 (59.3)	67 (79.0)	13 (25.7)	1	227 (290.7)
unsexed adult	13	3	59	74	36	51	3	1	239
juvenile	6 (14.3)	2 (14.8)	28 (59,3)	36	7	10 (33.1)	2 (9.9)	-	91 (138.5)
infant	5 (18.1)	1 (20.6)	67 (79.0)	51	10 (33.1)	17	- (14.9)	-	151 (180.5)
baby	- (4.9)	- (7.4)	13 (25.7)	3	2 (9.9)	- (14.9)	-	-	18 (67.2)
other	1	-	1	1	-	-	- (4.4)	1	4

TABLE 6.8 Frequency of reciprocal grooming interactions between the various classes.
(Figures in brackets are expected values were association between the classes random)

	mature male	young male	female	unsexed adult	juvenile	infant	baby	TOTAL
mature male	-	1	3	1	-	1	-	6 (15.8)
young male	1	-	2	2	1	1	-	7 (17.6)
female	3	2	13	19	8	9	1	55 (57.8)
unsexed adult	1	2	19	20	6	3	-	51
juvenile	-	1	8	6	1	-	-	16 (27.5)
infant	1	1	9	3	-	-	-	14 (35.9)
baby	-	-	1	-	-	-	-	1 (13.3)

FIG.6.9 Frequency of grooming interactions between the various classes, broken down to show the role of each class. (Expected values in brackets)

Recipient: / Groomer:	mature male	young male	female	unsexed adult	juvenile	infant	baby	TOTAL
Mature male	- (1.3)	3 (4.8)	3 (19.7)	3	- (8.6)	2 (10.9)	- (2.9)	11 (48.2)
young male	3 (4.8)	- (1.7)	6 (21.7)	2	2 (8.9)	1 (12.3)	- (4.4)	14 (53.8)
female	21 (19.7)	2 (21.7)	47 (69.0)	29	18 (35.5)	59 (47.4)	12 (15.4)	188 (208.7)
unsexed adult	11	3	49	94	25	46	2	230
juvenile	6 (8.6)	1 (8.9)	18 (35.5)	17	8 (8.5)	8 (19.8)	1 (5.9)	59 (87.2)
infant	4 (10.9)	1 (12.3)	17 (47.4)	8	2 (19.8)	17 (17.8)	- (8.9)	49 (117.1)
baby	- (2.9)	- (4.4)	2 (15.4)	1	1 (5.9)	- (8.9)	- (5.3)	4 (42.8)
TOTAL	45 (48.2)	10 (53.8)	142 (208.7)	154	56 (87.2)	133 (117.1)	15 (42.8)	555

of 221.9 with 4 degrees of freedom, which is highly significant ($p =<0.001$). Therefore the amount of grooming that the various classes did differs from what would be expected on a random basis. Almost half the total value of the X^2 is contributed by the discrepancy between observed and expected values for adults other than mature males; hence it seems safe to conclude that this category groomed more than expected, and other classes less.

Similarly comparing the observed totals for the columns with expected totals gives a X^2 of 38.75 with 4 degrees of freedom, which is again significant ($p =<0.001$). Thus the various classes did not all receive the amount of grooming expected. While departures from expectancy are less marked than in the previous case it appears that infants and adults other than mature males were groomed rather more than expected, and juveniles and babies less.

If interactions between the classes were random one would expect each class to assume the roles of groomer and recipient equally often. Perusal of the marginal totals in fig. 6.9 suggests that this was not the case. Not only did some classes groom or receive more grooming than expected, but the ratio of grooming given to grooming received appears in some

instances to depart from unity. For example mature males groomed other animals 11 times and were themselves groomed 45 times. Were they equally likely to assume either role in these 56 interactions the expected values for grooming both given and received would be 28. Comparison of observed and expected values gives a X^2 of 20.64 with one degree of freedom, for which p =<0.001. Hence we can conclude that mature males were more likely to be groomed than to groom in those interactions in which they were involved.

Similarly, it can be shown that infants also were more likely to be the recipients of grooming (X^2 = 38.77 with 1 d.f, p =<0.001), and the same may perhaps be true of babies (X^2 = 6.368 with 1 d.f, p =<0.05). On the other hand adults other than mature males were more likely to be groomers (X^2 = 25.87 with 1 d.f, p =<0.001). For juveniles, no difference either way can be shown (X^2 = 0.078).

Since the greatest departure from the expected frequency of grooming is found in adults other than mature males, it is worth considering this category in more detail to see whether the excess of grooming is distributed randomly over the classes or is selective. The table below shows the number of

times that adults other than mature males groomed the various classes, together with expected values, calculated from the probabilities in fig. 6.3 as proportions of 432, were they equally likely to groom all classes.

class groomed	MM	A-M	J	I	B	Total
observed	35	232	45	106	14	432
expected	40.4	187.4	73.1	98.1	32.7	432

X^2 is 33.46 with 4 degrees of freedom, for which $p =< 0.001$. Thus, given that adults other than mature males groomed other animals 432 times, this grooming was not distributed randomly. They appear to have groomed members of their own class more than expected, and juveniles and babies less.

Similarly, given that adults other than mature males were groomed 306 times, one can ask whether they were equally likely to be groomed by all classes. The next table gives observed and expected values for grooming of this category by the various classes.

class grooming	MM	A-M	J	I	B	Total
observed	9	232	36	26	3	306
expected	28.6	132.8	51.8	69.5	23.2	305.9

X^2 is 137.1 with 4 degrees of freedom, for which $p =< 0.001$, more than half this value being contributed

by the discrepancy between observed and expected values for adults other than mature males. Hence the groomers of adults other than mature males were not drawn randomly from the various classes; members of their own class groomed them more than expected and other classes less.

The case of infants is also of interest. These were groomed 133 times. Observed and expected values for grooming by the various classes are as follows:

class grooming:	MM	YM	F	UA	J	I	B	T
observed	2	1	59	46	8	17	-	133
expected	12.4	13.9	53.8		22.5	20.1	10.1	132.8

X^2 is 50.3 with 4 degrees of freedom (young males, females, and unsexed adults being combined into a single category), for which $p =<0.001$. Therefore the 133 groomers of infants were not drawn randomly from all classes; adults other than mature males groomed them more than expected, and other classes less. Much of this excess is likely to be due to grooming by females rather than young males, since the observed value for grooming by females is higher than the expected value even before unsexed adults are taken into account.

Essential aspects of the findings on participation in grooming sessions can be summarised as follows. Adults other than mature males both groomed and were themselves groomed more than expected on a random basis, and they were more likely to groom than to be groomed in those interactions in which they participated. Among other classes the most striking departure from expectancy was found in juveniles; these both groomed and were groomed far less than expected. Mature males were groomed about as often as expected, but groomed other classes less. Infants groomed less but themselves received rather more grooming than expected, largely as a result of an excess of grooming by adults other than mature males. Babies appeared both to groom and to be groomed less than expected, but this could at least in part be a result of the timorous behaviour of females with babies (see p.226).

The relative proportions of females and young males in the interactions involving adults other than mature males cannot be determined, but in interactions with infants it seems likely that the majority would have been females; in only one of the 119 instances was the participant definitely identified as a young male. This does not necessarily

mean that all were mother/infant interactions ... while it was not always possible to decide what the relationship between a female and an infant was, infants were certainly groomed sometimes by females other than their mothers ... but this would be true of a fair proportion. Likewise one can tentatively suggest that a large proportion of the interactions among adults other than mature males will have been female/female interactions.

The salient features of the distribution of grooming in these blue monkey groups would appear, therefore, to be a superfluity of female/infant and perhaps of female/female interactions, and a short-fall in the participation of juveniles. Males, or at least mature males, did not play a prominent role in grooming. This differs from the pattern in many other species. In C.aethiops, for instance, Gartlan (1966) found that while all classes were equally likely to be involved in social grooming, adult females were involved less with other females than would be expected, and more with adult males. Likewise in a group of black mangabeys adult male/adult female interactions were much more numerous than expected (Chalmers 1968b). On the other hand Sugiyama (1965 b) found that males in langur one-

male-groups took little part in grooming.

(b) Initiation of grooming.

The initiation of grooming interactions was observed in 333 cases. In 103 of these the two participants in the interaction were already sitting together at its start. These data are considered elsewhere with similar information from other sources (see p.327). In a further 230 cases one animal was seen to approach the other. Fig. 6.10 shows the number of times the various classes approached one another, with expected values, calculated from the probabilities in fig. 6.2, were the 230 approaches distributed at random. Totals for the rows give the number of approaches made by each class, and totals for the columns the number of times each class was approached.

X^2 for the row totals, combining young males, females, and unsexed adults, is 5.375 with 4 degrees of freedom, which is not significant. Hence we can conclude that the numbers of observed approaches by each class do not differ significantly from what would be expected on a random basis.

When the outcome of these approaches is considered, though, differences between the classes are

FIG.6.10 Numbers of times the various classes were seen to approach one another prior to grooming. (Expected values in brackets).

Class approached: / Class approaching:	mature male	young male	female	unsexed adult	juvenile	infant	baby	TOTAL
mature male	1 (0.5)	1 (2.0)	10 (8.2)	4	1 (3.6)	2 (4.5)	- (1.2)	19 (20.0)
young male	1 (2.0)	- (0.7)	2 (9.0)	1	1 (3.7)	- (5.1)	- (1.8)	5 (22.3)
female	5 (8.2)	- (9.0)	19 (28.6)	22	3 (14.7)	4 (19.6)	- (6.4)	53 (86.5)
unsexed adult	4	-	12	26	3	5	-	50
juvenile	3 (3.6)	1 (3.7)	10 (14.7)	13	4 (3.5)	3 (8.2)	1 (2.5)	35 (36.2)
infant	2 (4.5)	- (5.1)	25 (19.6)	15	6 (8.2)	10 (7.4)	- (3.7)	58 (48.5)
baby	- (1.2)	- (1.8)	8 (6.4)	1	1 (2.5)	- (3.7)	- (2.2)	10 (17.8)
TOTAL	16 (20.0)	2 (22.3)	86 (86.5)	82	19 (36.2)	24 (48.5)	1 (17.8)	230

revealed. The table below gives the number of occasions on which the various classes received grooming invitations or solicited grooming themselves after approaching, together with expected values (in brackets) were there no relation between class of the approacher and outcome of the approach.

class approaching:	MM	YM	F	UA	J	I	B	T
receives g.i.	1 (5)	3 (1.3)	16 (13.8)	13 (13)	19 (9.1)	7 (15.1)	1 (2.6)	60
gives g.i.	18 (14)	2 (3.7)	37 (39.2)	37 (37)	16 (25.9)	51 (42.9)	9 (7.4)	170

Combining young males, females, and unsexed adults, X^2 is calculated as 26.66 with 4 degrees of freedom, which is highly significant ($p =<0.001$). Thus although all classes were equally likely to approach other animals the outcome of these approaches differed. Mature males, infants and babies were rather more likely to give grooming invitations than other classes, and juveniles more likely to have grooming invitations directed to them.

Comparing the totals for the columns in fig. 6.10 with expected values yields a X^2 of 71.6 with 4 degrees of freedom (adults other than mature males being treated as a single category), which is highly significant ($p =<0.001$). Therefore the various

classes were not approached at random. Mature males appear to have been approached about as often as expected, but other adults more often and the remaining classes less often.

Below are shown the outcome of approaches in relation to the class of the animal approached, with expected values (in brackets) were there no association between class and the outcome of approaches.

class approached:	MM	YM	F	UA	J	I	B	T
receives g.i.	8 (11.8)	2 (1.5)	69 (63.5)	68 (60.6)	10 (14)	13 (17.7)	- (0.7)	170
gives g.i.	8 (4.2)	- (0.5)	17 (22.5)	14 (21.4)	9 (5)	11 (6.3)	1 (0.3)	60

Combining adults other than mature males into a single category, and lumping infants and babies together to eliminate low expected values, $X^2 = 20.87$ with 3 degrees of freedom, for which $p =< 0.001$. Thus the outcome of an approach differed depending on the class of the animal approached; adults other than mature males were more likely to have grooming invitations directed to them than were other classes.

A total of 415 grooming invitations were observed. In a further 69 cases one animal started grooming another without any obvious invitation being

given. The table below shows the number of invitations given by each class, with expected values, calculated as proportions of 415 from the marginal probabilities in fig. 6.2, were all classes equally likely to give invitations.

class giving invitation:	MM	YM	F	UA	J	I	B	T
observed	36	10	107	113	48	90	11	415
expected	36.5	39.8	156.5		65.6	87.6	29.0	415

Combining adults other than mature males together X^2 is 21.75 with 4 degrees of freedom, for which $p = <0.001$. However more than half this value is contributed by the discrepancy between observed and expected scores for babies; it should hence be treated with reserve (see p.226). Departures from expectancy among the other classes are less marked.

On the other hand, comparison of observed numbers of invitations directed <u>to</u> the various classes with expected values were all given invitations at random reveals pronounced discrepancies.

class given invitation:	MM	YM	F	UA	J	I	B	T
observed	15	8	159	148	40	42	3	415
expected	36.5	39.8	156.5		65.6	87.6	29.0	415

X^2 is 141.5 with 4 degrees of freedom (young males, females, and unsexed adults being combined as before), for which p =<0.001. Adults other than mature males received more invitations than expected, and other classes less. Since the observed value for females slightly exceeds the expected value even before the 148 invitations directed to unsexed adults are taken into account, it is likely that females rather than young males were the recipients of much of this surplus of invitations.

Fig. 6.11 shows the number of times each class was seen to adopt the different types of posture in soliciting grooming, together with expected values were there no association between class and the posture used. As it stands the table is not amenable to statistical analysis since many expected values are below 5. If, however, young males, females, and unsexed adults are combined into one class and infants and babies into another, and the 'standing facing away', 'standing with head low', and 'other' rows are amalgamated, a 4 X 5 table with only one expected value below 5 is obtained. X^2 is calculated as 30.21 with 12 degrees of freedom, for which p =<0.01. Thus there is a slight association between class and the postures used to solicit

grooming. In particular infants and babies appear to have solicited grooming by lying more often than expected, and other classes less often.

Fig. 6.12 shows the number of times the various postures were directed <u>to</u> particular classes, with expected values were there no relation between posture and the class from which grooming was solicited. Lumping all adults together, and combining infants and babies and the bottom three rows as above, gives a 3 X 5 table with only two expected values below 5. X^2 is calculated as 8.235 with 8 degrees of freedom, which is not significant. Hence the posture used to solicit grooming did not vary with the class to which the invitation was directed.

Of the 415 grooming invitations observed, 315 were successful and 100 unsuccessful. Fig. 6.13 gives the number of times each type of posture both elicited and failed to elicit grooming, with expected values were there no differences in the effectiveness of the various types of invitation. X^2 is 11.53 with 6 degrees of freedom, which is not significant. Hence there is no relation between the posture used and the success of the invitation.

The table below shows the number of times grooming invitations given by the various classes

FIG.6.11 Postures adopted by the various classes when soliciting grooming.

(Figures in brackets are expected values were there no association between class and posture)

Class soliciting grooming:	mature male	young male	female	unsexed adult	juvenile	infant	baby	TOTAL
Posture:								
half crouch	12 (10.4)	4 (2.9)	32 (30.9)	39 (32.7)	12 (13.9)	19 (26.0)	2 (3.2)	120
lie	5 (11.4)	3 (3.2)	27 (33.8)	29 (35.7)	21 (15.1)	40 (28.1)	6 (3.5)	131
sit with head low	8 (5.3)	2 (1.5)	18 (15.7)	21 (16.6)	2 (7.1)	10 (13.2)	- (1.6)	61
sit with head back	4 (3.9)	1 (1.1)	12 (11.6)	11 (12.2)	8 (5.2)	9 (9.8)	- (1.2)	45
stand with tail raised	1 (2.0)	- (0.6)	8 (5.9)	5 (6.3)	4 (2.7)	5 (5.0)	- (0.6)	23
stand with head low	2 (1.7)	- (0.5)	8 (5.1)	5 (5.4)	1 (2.3)	3 (4.3)	1 (0.5)	20
others	4 (1.3)	- (0.4)	2 (3.9)	3 (4.1)	- (1.7)	4 (3.2)	2 (0.4)	15
TOTAL	36	10	107	113	48	90	11	415

FIG.6.12 Postures adopted when soliciting grooming from the various classes.
(Figures in brackets are expected values were there no association between the posture adopted and the class of the animal from which grooming is solicited)

Class receiving invitation: / Posture:	mature male	young male	female	unsexed adult	juvenile	infant	baby	TOTAL
half crouch	6 (4.3)	4 (2.3)	34 (46.0)	49 (42.8)	13 (11.6)	12 (12.1)	2 (0.9)	120
lie	5 (4.7)	2 (2.5)	61 (50.2)	46 (46.7)	6 (12.6)	11 (13.3)	- (0.9)	131
sit with head low	1 (2.2)	1 (1.2)	23 (23.4)	20 (21.7)	8 (5.9)	8 (6.2)	- (0.4)	61
sit with head back	- (1.6)	- (0.9)	17 (17.2)	16 (16.0)	6 (4.3)	5 (4.6)	1 (0.3)	45
stand with tail raised	1 (0.8)	- (0.4)	11 (8.8)	7 (8.2)	2 (2.2)	2 (2.3)	- (0.2)	23
stand with head low	2 (0.7)	1 (0.4)	7 (7.6)	7 (7.1)	2 (1.9)	1 (2.0)	- (0.1)	20
others	- (0.5)	- (0.3)	6 (5.7)	3 (5.3)	3 (1.4)	3 (1.5)	- (0.1)	15
TOTAL	15	8	159	148	40	42	3	415

FIG.6.13 Comparison of success rates of different types of grooming invitation.

(Figures in brackets are expected values were there no association between the posture adopted and the success of the invitation)

Posture:	Successful	Unsuccessful	TOTAL
half crouch	87 (91.0)	33 (29.0)	120
lie	93 (99.4)	38 (31.6)	131
sit with head low	55 (46.3)	6 (14.7)	61
sit with head back	32 (34.2)	13 (10.8)	45
stand with tail raised	19 (17.5)	4 (5.5)	23
stand with head low	16 (15.2)	4 (4.8)	20
others	13 (11.4)	2 (3.6)	15
TOTAL	315	100	415

were successful or otherwise, irrespective of type, with expected values (in brackets) based on the assumption that there was no difference between classes in this respect.

class giving invitation:	MM	YM	F	UA	J	I	B	T
successful	32 (27.3)	7 (7.6)	86 (81.2)	81 (85.8)	32 (36.4)	68 (68.3)	9 (8.3)	315
unsuccessful	4 (8.7)	3 (2.4)	21 (25.8)	32 (27.2)	16 (11.6)	22 (21.7)	2 (2.7)	100

Combining adults other than mature males into a single category X^2 is 5.78 with 4 degrees of freedom, which is not significant. Hence there was no relation between the success of a grooming invitation and the class of the animal giving it.

If the success of grooming invitations is analysed in relation to the class to which they were directed, though, a different picture emerges.

class rec'ng invitation:	MM	YM	F	UA	J	I	B	T
successful	6 (11.4)	6 (6.1)	123 (120.7)	117 (112.3)	32 (30.4)	28 (31.9)	3 (2.3)	315
unsuccessful	9 (3.6)	2 (1.9)	36 (38.8)	31 (35.7)	8 (9.6)	14 (10.1)	- (0.7)	100

Combining young males, females, and unsexed adults into a single category and infants and babies into another, X^2 is 12.98 with 3 degrees of freedom, for

which p =<0.01. Thus the outcome of a grooming invitation was to some extent related to the class of the animal to which it was given; adults other than mature males appeared to respond more often than one would expect, and other classes less often.

On 69 occasions one animal started to groom another without any obvious invitation being given. The number of occasions on which each class was groomed without giving an invitation, with expected values, from the marginal probabilities in fig. 6.2, were all classes equally likely to be so groomed, are given below.

class groomed:	MM	YM	F	UA	J	I	B	T
observed	5	1	21	18	4	18	2	69
expected	6.1	6.6	26.0		10.9	14.6	4.8	69

Combining young males, females, and unsexed adults, X^2 is 8.67 with 4 degrees of freedom, which is not significant. Therefore the frequency with which the various classes were groomed without having given a grooming invitation does not differ from what would be expected on a random basis.

The next table shows the number of times each class started to groom another animal without an invitation having been given, with expected values were this behaviour distributed randomly among the classes.

class grooming:	MM	YM	F	UA	J	I	B	T
observed	1	2	22	17	17	9	1	69
expected	6.1	6.6	26.0		10.9	14.6	4.8	69

X^2 is 15.0 with 4 degrees of freedom (young males, females and unsexed adults being combined as before), for which p =<0.01. Thus this behaviour is not distributed entirely at random; it would appear that adults other than mature males were rather more likely to start grooming without an invitation, and other classes less so.

We are now in a position to account for certain aspects of the non-random distribution of grooming. It has been shown that while there were no clear cut differences in the likelyhood of each class approaching other animals, adults other than mature males were more likely to be approached than were other classes. (They were more likely also to sit with other animals ... see below, p.326). In addition they were more likely to have grooming invitations directed to them when approached. These factors result in their receiving a disproportionately large number of invitations. While all classes were equally successful in soliciting grooming, adults other than mature males were rather more likely to respond positively to grooming invitations. Hence

the excess of grooming by adults other than mature males is accounted for primarily by the behaviour of animals soliciting grooming from them, and to a lesser extent by their reaction to grooming invitations.

(c) Duration of grooming sessions.

The approximate durations of grooming sessions were recorded in 350 instances. Fig. 6.14 shows the number of occasions on which each class groomed for particular lengths of time. Since timing of sessions was only approximate calculation and comparison of means and standard deviations for each class would be inappropriate. The data have therefore to be analysed in other ways. Compressing fig. 6.14 yields the 2 X 3 table below:

Class of Groomer:	all adults	J	I & B	T
Duration:				
less than 1 min.	108 (111.5)	19 (16.7)	16 (14.7)	143
more than 1 min.	165 (161.5)	22 (24.3)	20 (21.3)	207
Total	273	41	36	350

The expected values in parenthesis were calculated on the assumption that there was no relation between class of groomer and the duration of grooming. The

extreme degree of lumping is necessary to eliminate expected values below 5. X^2 is 0.891 with 2 degrees of freedom, which is not significant. Thus the duration of grooming sessions appears to be unrelated to the class of the groomer.

Similarly fig. 6.15 gives the number of times each class groomed for particular periods. Appropriate combination of categories yields the following table:

Class of recipient:	MM	A-M	J	I & B	T
Duration less than 1 min.	17 (13.9)	70 (75.6)	17 (14.7)	39 (38.8)	143
more than 1 min.	17 (20.1)	115 (109.4)	19 (21.3)	56 (56.2)	207
Total	34	185	36	95	350

X^2 is 2.48 with 3 degrees of freedom, which is not significant. Hence it appears that the duration of grooming sessions bears no relation to the class of the animal being groomed.

(d) Termination of grooming.

The termination of grooming was recorded on 388 occasions. On 334 of these the session was ended by the animal grooming, and on 54 by the recipient. The

FIG.6.14 Duration of grooming sessions, analysed by class of groomer.

Groomer:	mature male	young male	female	unsexed adult	juvenile	infant	baby	TOTAL
Duration:								
< 1 min.	3	2	56	47	19	16	-	143
1 - 2 mins.	2	2	24	24	6	3	2	63
2 - 3 mins.	1	-	16	24	5	2	-	48
3 - 4 mins.	1	2	6	8	1	6	-	24
4 - 5 mins.	-	-	13	10	6	3	-	32
> 5 mins.	1	-	17	14	4	4	-	40
TOTAL	8	6	132	127	41	34	2	350

FIG.6.15 Duration of grooming sessions, analysed by class of recipient.

Recipient: / Duration:	mature male	young male	female	unsexed adult	juvenile	infant	baby	TOTAL
< 1 min.	17	3	32	35	17	32	7	143
1 - 2 mins.	5	-	14	17	7	19	1	63
2 - 3 mins.	2	2	11	15	5	10	3	48
3 - 4 mins.	5	1	7	5	3	3	-	24
4 - 5 mins.	2	1	9	7	4	9	-	32
> 5 mins.	3	-	18	8	-	11	-	40
TOTAL	34	7	91	87	36	84	11	350

table below shows the number of times each class was the groomer in these 388 interactions, together with the number terminated and expected values were all classes equally likely to stop grooming.

Class:	MM	YM	F	UA	J	I	B	T
grooms in:	8	7	136	146	49	38	4	388
terminates:	7 (6.9)	7 (6.0)	112 (117.1)	125 (125.7)	45 (42.2)	35 (32.7)	3 (3.4)	334

Combining young males, females, and unsexed adults, X^2 is 0.489 with 4 degrees of freedom, which is not significant. Therefore there is no association between the class of the animal grooming and the chances of it terminating the session.

Likewise the next table shows the number of occasions each class was the recipient in these sessions, with the number terminated and expected values were all classes equally likely to end sessions in which they were being groomed.

Class:	MM	YM	F	UA	J	I	B	T
recipient in :	36	5	95	98	37	107	10	388
terminates:	5 (5)	- (0.7)	10 (13.2)	9 (13.6)	6 (5.1)	21 (14.9)	3 (1.4)	54

Combining adults other than mature males together X^2 is 7.12 with 4 degrees of freedom, which is not

significant. Hence there is no association between the class of the animal being groomed and the chances of it ending the session.

On 198 occasions pairs were seen to remain sitting together after an interaction involving grooming or unsuccessful grooming invitations. In a further 247 they moved apart. The chances of a pair remaining together appear to be unaffected by whether grooming has taken place or not. The table below shows the number of times pairs remained together or moved apart with or without having groomed.

	Sit together	Move apart	Total
Grooming	180	223	403
No grooming	18	24	42
Total	198	247	445

X^2 calculated with correction for continuity is 0.041 with one degree of freedom, which is not significant.

Discussion.

The pattern of grooming among individuals or classes within a group is generally considered to reflect in some way the nature of the relationships between them. The precise interpretation placed on it is seldom explicit, however, and varies from one

study to another and even within studies. For instance Hall and DeVore (1965) state of savanna-living baboons: 'The nature of the dominance relations within a group are reflected in the amount of grooming attention an individual receives ... Nevertheless, it seems that all members of the group to some extent receive and give grooming attention, and the function of grooming is assumed to be not simply a cleaning of the body surface but a continuing reinforcement of the social bonds'. In groups that can be described as having a hierarchical structure it may well be found that grooming interactions fit in with such a pattern. For example a 'dominant, central male' in a baboon troop receives more grooming attention than a 'peripheral or less dominant male', (Hall and DeVore 1965), and the unit leader in the hamadryas one-male-group is groomed by his females far more than he grooms them (Kummer 1968). Yet while contrasts in the amount of grooming received may coincide with differences in rank they cannot be taken as proof of the existence of such gradations. This distinction is clarified by Rowell (1966b); she points out that only social interactions of the approach/retreat pattern can be used to <u>determine</u> rank. Other types of interaction cannot, even though their distribution may

subsequently be shown to be related to a hierarchy determined by consideration of approach/retreat interactions. Even in groups with an apparently well defined rank order much grooming cannot be correlated with the hierarchy. Grooming between females and infants, for instance, could not be interpreted in the same way as grooming between adults.

Since social grooming takes place under a diversity of circumstances one may well be mistaken in seeking a unitary explanation. As Sparks (1967) points out, grooming of the young is a characteristic pattern of parental behaviour in most mammals but allogrooming among adults is highly developed only in primates. It may therefore be misleading to consider grooming of infants by females and grooming between adults within the same narrow theoretical framework. Furthermore the significance of grooming may differ from one species to another. The observed pattern will represent the outcome of a variety of different and possibly competing tendencies. For instance Van Lawick-Goodall (1968) found that ' ... the partner selected by any one individual chimpanzee for social grooming depended partly on the rank of the individual concerned, partly on the oestrous condition of females, and partly on individual preferences'.

A further complication is that the number of grooming interactions that actually occur may be affected not only by the relationship between the two animals directly concerned but also by their relations with other individuals. For instance Kummer (1968) states of the hamadryas that ' ... juvenile females eagerly strive to groom their leader but are successful in doing so only when no adult female is grooming him'. Figures for the frequency of grooming between adult males and juvenile females would therefore be misleading if taken at face value.

Sparks (1967) suggests that soliciting of grooming by dominant animals may, in certain contexts, serve to reduce avoidance responses in subordinate individuals by arousing behaviour incompatible with fear and aggression, and thus promote group cohesion in troops with a marked dominance hierarchy. If this hypothesis is of universal applicability, he points out, grooming should be less frequent in species which do not have a steep 'dominance gradient' between individuals. Leaving aside the difficulty of making anything other than very approximate comparisons of the frequency of grooming in different species, this

generalisation does not stand up to detailed scrutiny. As Sparks himself admits, the observations of Jay (1965) on langurs and Simmons (1965) on bonnet macaques do not fit in with it, nor is it supported by my own observations on blue monkeys.

The commonest interpretation of social grooming is that it serves in some way to maintain or reinforce social bonds between the individuals concerned. Van Lawick-Goodall (1968), for example, describes how grooming sessions between mother chimps and their offspring become longer and relatively more frequent as the young become more independent and rise in status. Similarly Kummer (1968) suggests that grooming in the hamadryas may be used to strengthen a social bond when it is in danger of breaking apart; for example an old male was never seen to groom his females when he had seven, but frequently did so when he had lost all but two.

If the reinforcement of social bonds is considered as being the primary function of grooming, the interpretation of frequencies of interaction is still far from straightforward. On the one hand it could be argued that grooming would be most common between those individuals most likely to break apart from one another, in which case the frequency of

grooming would be inversely proportional to the strength of the bonds concerned. Alternatively one could argue that the strongest bonds would need the most grooming to maintain them, in which case grooming frequencies would provide a direct measure of the affinity of the participants. This latter is perhaps the more plausible alternative. It should be evident, though, from the preceding discussion, that to consider frequencies of grooming simply as indicative of the strength of some underlying affinity may well be an oversimplification.

How then is the pattern of grooming in the blue monkey to be interpreted? The safest conclusion would seem to be that frequencies of grooming by themselves tell one little; only when considered in conjunction with other behavioural evidence do they assume any great significance.

'MOUTHING' BEHAVIOUR.

This pattern of behaviour was occasionally seen when one monkey approached another. The one monkey would walk up to the other and bring its mouth up to the others' from below, sometimes appearing to sniff it (see fig. 6.16). A partially crouched position was often but by no means invariably

assumed when performing the movement. The monkey to which the behaviour was directed either turned its head aside, whereupon it might be repeated, or else showed little obvious reaction. In only three instances did it move away.

Mouthing was observed 56 times. In all but three it was given by one animal that had just approached another. In 13 cases it was associated with grooming; in 9 of these the animal giving the movement then groomed the other, and in a further 4 it was groomed itself. The movement was followed by play on one occasion, and in another 10 cases the animals concerned remained sitting together but without any obvious further interaction. In the remaining 22 they moved apart.

The occurrence of mouthing behaviour between the various classes, with expected values, from the marginal probabilities in fig. 6.2, were it distributed at random, are shown in fig. 6.17. The figures suggest that the movement is generally directed by young animals to adults rather than the reverse. While the numbers involved are too small to reach hard and fast conclusions, statistical analysis lends some support to this impression. Comparison of observed and expected row totals, combining all adults into one category and infants and babies into another, gives

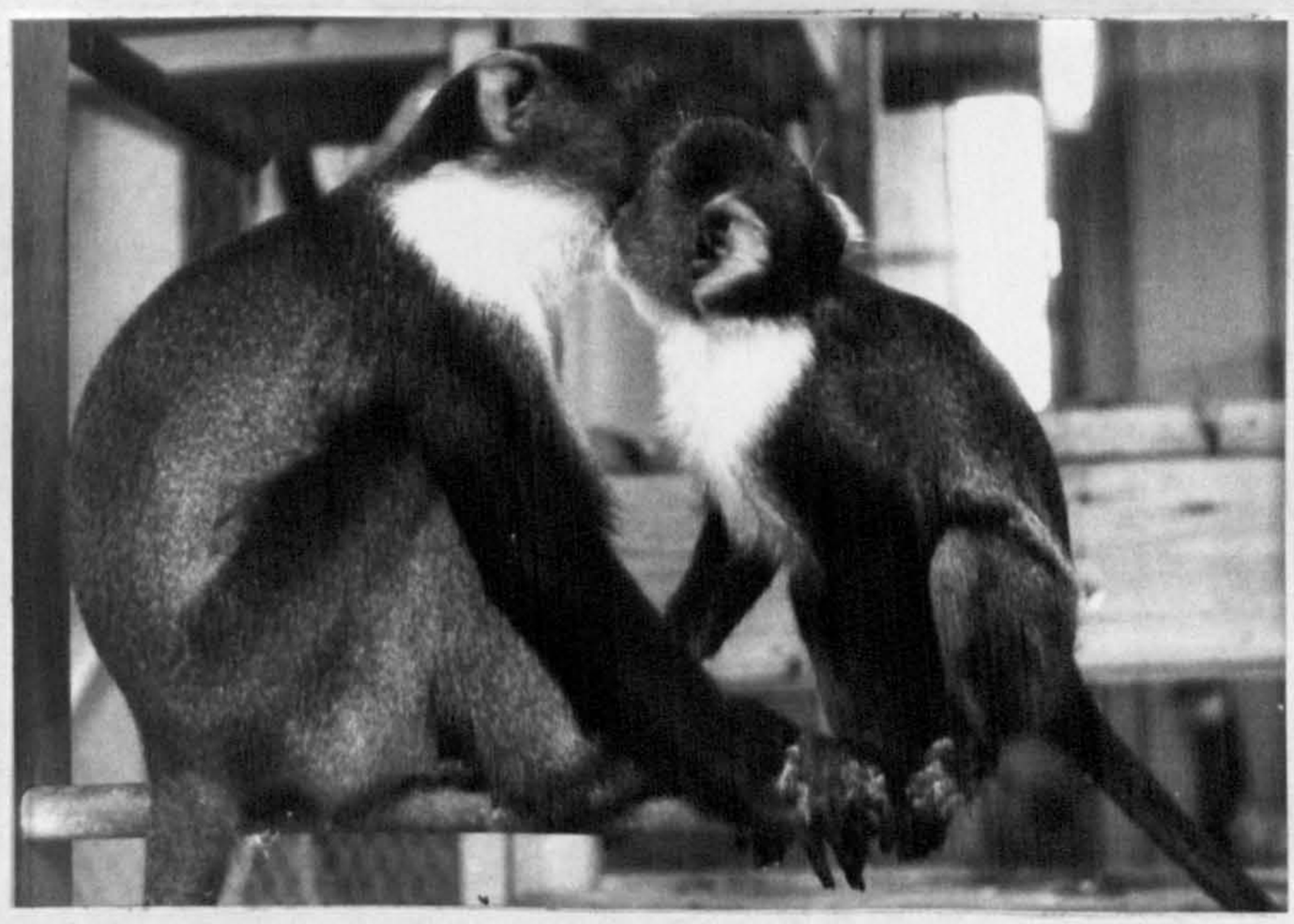


FIG.6.16 'Mouthing' behaviour. An infant Sykes monkey mouthing an adult (above), and an adult mouthing another of the same class (below).

FIG.6.17 Frequency of 'mouthing' behaviour between the various classes.

(Expected values in brackets)

Recipient:	mature male	young male	female	unsexed adult	juvenile	infant	baby	TOTAL
Performer: mature male	-	-	1	1	1	-	-	3 (4.9)
young male	-	-	-	-	-	-	-	- (5.3)
female	3	1	4	-	-	1	-	9 (21.1)
unsexed adult	1	-	1	6	-	1	-	9
juvenile	-	-	2	7	-	2	-	11 (8.8)
infant	-	-	7	7	4	2	-	20 (11.8)
baby	-	-	2	1	1	-	-	4 (3.9)
TOTAL	4 (3.9)	1 (5.3)	17 (21.1)	22	6 (8.8)	6 (11.8)	- (3.9)	56

a X^2 of 8.327 with 2 degrees of freedom for which $p =< 0.05$, suggesting that the various categories differ in their likelihood of performing the movement. Similarly comparison of observed and expected column totals yields a X^2 of 12.037 with 2 degrees of freedom, for which $p =< 0.01$. Hence the classes differ in the chances of having this behaviour directed to them.

The significance of mouthing behaviour is not clear. Gartlan (1966) describes a similar pattern of behaviour in C.aethiops, often shown by infants to their mothers and sometimes by other classes, usually juveniles or subadults. In certain cases it apparently served to identify the food the recipient had been eating. For instance, Gartlan relates how an infant approached a juvenile that had been feeding on highly scented Saba flowers, mouthed it, and then moved 30 yards to the nearest flowering Saba plant and ate flowers itself. The same interpretation could in some cases be placed on mouthing in C.mitis. In 22 of the 56 instances the animal to which the movement was directed had just been feeding, or had full cheek pouches. In 4 cases the animal that performed the movement then moved away and fed on the same plant as the recipient, and in a further

instance walked over to a fruit of the same species and sniffed it, but did not eat it.

Gartlan suggests that the infant behaviour pattern may have become ritualised as a 'greeting'. He points out that ' ... the close approach of another animal, especially of adult animals by juveniles, often seemed to involve an element of fear, and under these circumstances mouthing was common'. Comparable patterns of behaviour are found in other species. Van Lawick-Goodall, for instance, describes a variety of 'submissive' postures given by approaching animals in the chimpanzee, and lipsmacking, presumably derived from lipsmacking during grooming, is frequently given as a prelude to close approach and more elaborate 'greetings behaviour" in baboons (Hall and DeVore 1965).

The extent to which such an interpretation can be placed on mouthing in the blue monkey is uncertain. In a few cases the animals approaching did appear tentative or fearful, as the following examples illustrate:

(i) An infant is eating Cynometra pods. A juvenile drops onto the same branch 5 ft from it. The infant leaps away 3 ft, then turns round, walks slowly up to the juvenile, and puts its mouth to the juvenile's. The latter moves away and eats Cynometra pods, and the infant resumes feeding also.

(ii) A female walks up to a second female and sits by it. As it does so the second jumps away 4 ft, crouches, and stares at it. The first female remains sitting and does not look at the second. After 15 secs the latter walks up to the first female and puts its mouth to hers. The first female gives a grooming invitation, and the second does likewise. Neither grooms the other, and after a minute the second female moves away 4 ft and sits.

However incidents such as these were exceptional. Approach was typically rapid and direct, and mouthing might be persistently repeated if the other animal turned aside. One could consider the adoption of a partially crouched posture to be indicative of submissiveness, but it may in the first instance be necessitated largely by the mechanics of the situation. If one monkey is sitting in the typical manner with its head slightly forward another cannot make mouth to mouth contact without assuming such a posture, unless it is very much smaller than the first animal. Infants seldom crouched when mouthing adults, and a small adult female was once seen to stand on its hind legs to mouth a mature male sitting further up a sloping branch.

In captive groups of C.albogularis mouthing was directed to newly introduced animals by other members of the group, and was also seen at other

times, particularly during feeding periods. These observations lend support to the view that mouthing is in origin a means of determining what another animal has been eating ... as such it might be of adaptive value in helping infants to discover what plants were edible ... but has come to assume other functions during the course of evolution.

Chapter 7

SOCIAL BEHAVIOUR III

SEXUAL BEHAVIOUR.

Sexual activity is an obtrusive feature of the behaviour of many species of primate, so much so that Buffon was moved to remark of the baboon that it was 'characterised by an extreme lasciviousness'. In contrast the behaviour of the blue monkey could hardly offend even the most puritanical; interactions involving mounting were seen only 31 times during the 20 months of the study. Such reticence may be a feature of other forest Cercopithecus spp; Haddow (1952), for example, failed to observe copulation in C.aethiops and concluded that it must take place at night.

Of the 31 mountings observed 15 were of adults by adults, including 11 of females by mature males, 3 of females by young males, and one of an unsexed adult by another of the same category (probably a young male and a female). The remaining 16 were made up of two mountings of juveniles by unsexed adults, one each of adult females and juveniles by juveniles, two each of unsexed adults and infants by juveniles and of juveniles by infants, and 6 of infants by infants. One of the interactions between a juvenile and an unsexed adult involved reciprocal

mounting; the adult mounted the juvenile and the latter in turn mounted the adult. This must therefore have entailed either a homosexual mounting or the mounting of a male by a female.

In most field studies it has proved possible to determine whether intromission has taken place during a mount, and in some cases whether or not ejaculation has occurred. This was seldom so with the blue monkey. Conditions of observation precluded the detection of ejaculate on the female's vulva following a mount, and there was no clear cut ejaculatory pause. Nevertheless it seems likely that most if not all of the mountings between adults can be considered as true copulations, and the same may apply to some of those involving juveniles.

Copulation may be initiated by either sex. In 5 of the 15 interactions between adults the female was seen to approach the male, and in 6 the male approached the female. Clear cut soliciting of copulation by the female, though, was seen on only two occasions. The female walked up to the male and stood about a foot away with limbs slightly flexed. In one case the tail was held high and the female looked back over her shoulder at the male, and in the other she looked straight ahead and the tail was held

low. In two further cases the female stood up and assumed the latter position when a male approached her, and in another two she did so when the male approached and touched her on the rump. In 3 of the remaining 9 cases the female did not appear to assume any special posture prior to copulation, and in the other 6 conditions of observation were too poor to determine whether she did or not.

The position assumed by the male during mounting is shown in fig. 7.1. The male grips the female's hind legs, just above the ankles, with his feet, and grasps the fur on her back with his hands. A similar position is assumed during copulation by male C.aethiops (Gartlan 1966) and C.ascanius (pers.obs.). Pelvic thrusts may be given at a rate of up to one per 2/3 secs. Mean duration of mounts by mature and young males was 9.7 secs, the longest lasting for 20 secs. As a rule the female remained still during copulation, but in three cases she walked slowly forward. In one of these, copulation was terminated by her losing her footing and both animals falling off the branch.

Most copulations involved only a single mounting, but in three cases the male mounted twice within a few seconds and in one there was a series of three

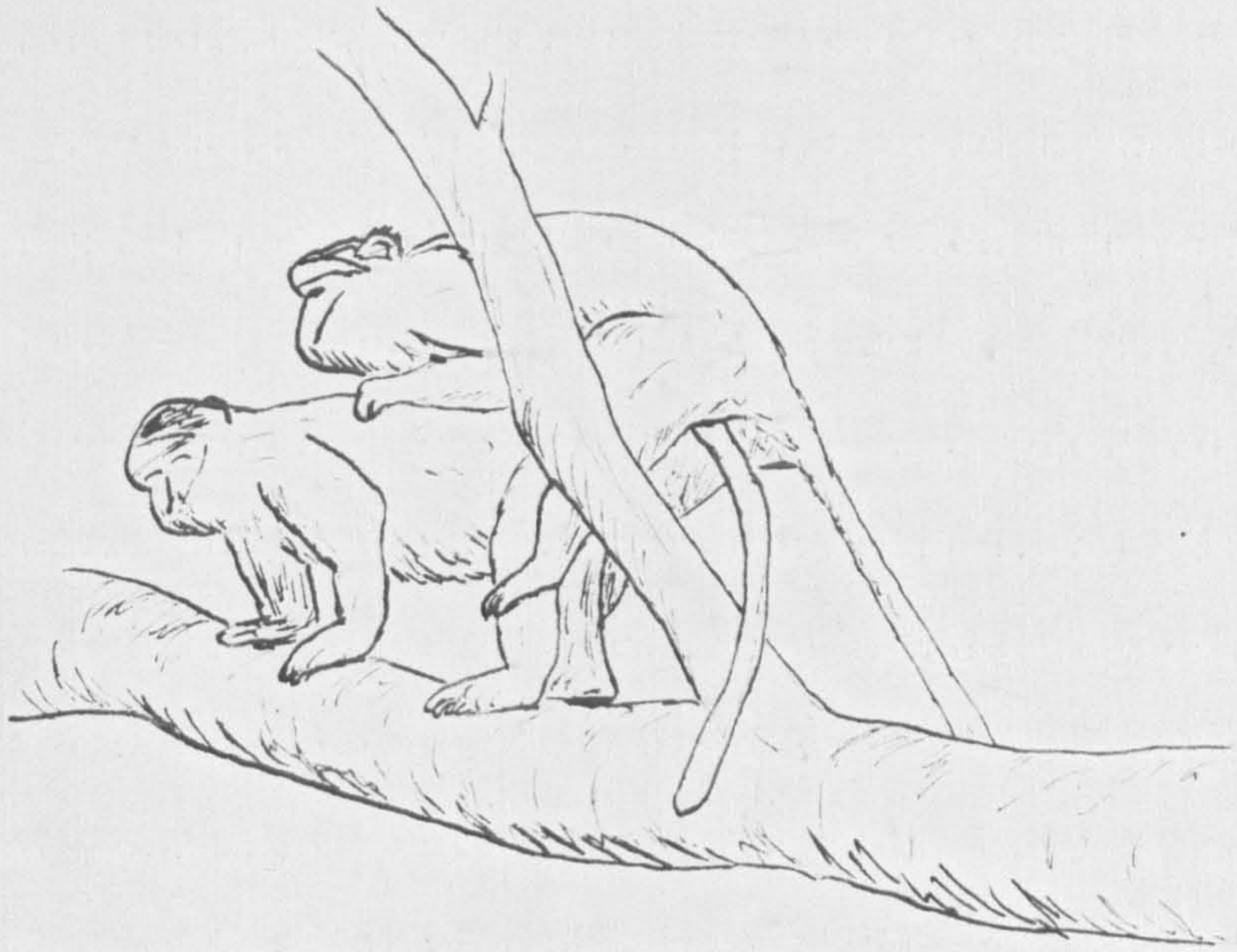


FIG. 7.1 A MATURE MALE MOUNTING A FEMALE

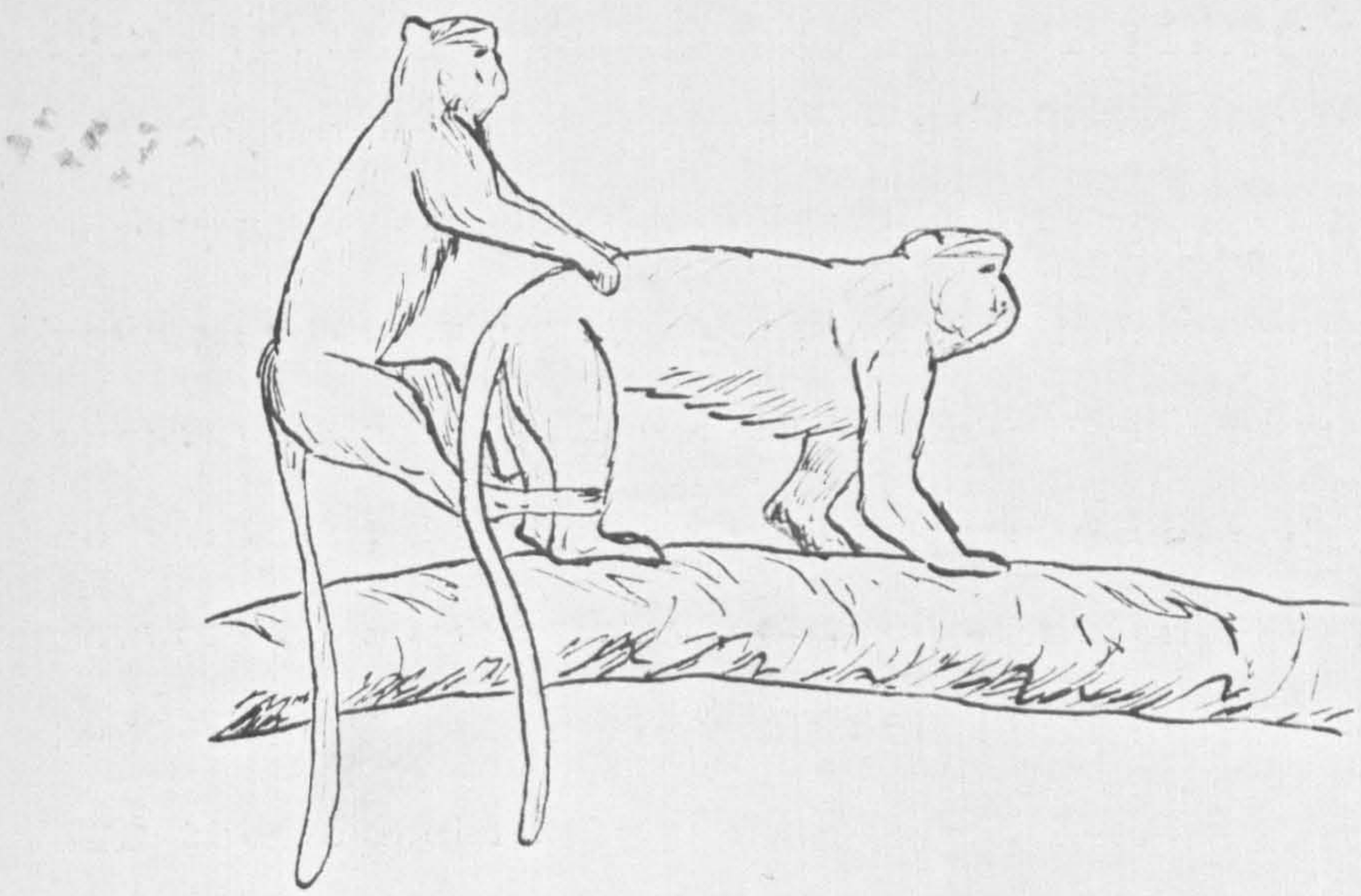


FIG. 7.2 A JUVENILE TRYING TO MOUNT A FEMALE

mountings, the female soliciting prior to each mounting and pelvic thrusts being observed only during the last. Single mountings are characteristic of the vervet (Gartlan 1966), whereas in other Cercopithecines such as rhesus (Altmann 1962) and some baboons (in S.Africa but not in Kenya, Hall and DeVore 1965) a series of mountings is the rule.

In 7 instances the female groomed the male when he dismounted, and in another 4 she at once ran off. In the remainder she moved away slowly.

Other monkeys in the vicinity of the copulating couple seldom showed any obvious reaction. One of the two mature males in group A once copulated within 20 ft. of the other without it appearing to take any notice. On two occasions a juvenile or small adult struck at the male and female from 1 - 4 ft away and made short rushes at them while copulation was in progress, but ran off as soon as the male dismounted. Similar 'harassing' behaviour by young animals was recorded on one occasion in C.aethiops (Gartlan 1969), and may be seen also in Papio anubis (pers.obs.).

Mountings by juveniles and infants differed from those by adults in that they did not always include all the features of adult copulation, and were generally of shorter duration. Thus of 6 mountings by

juveniles the correct position was attained in only three, and pelvic thrusts were given in only two. Mean duration of mounts was 5.25 secs, the longest being 15 secs. Likewise of 8 mountings by infants the correct position was attained in 5 and pelvic thrusts were given in 4. Mean duration was 4.25 secs, and the longest mounting lasted 10 secs.

In some cases failure to attain the typical adult position was due as much to lack of cooperation by the animal being mounted as to inexpertise on the part of the young monkey. As a rule animals mounted by juveniles or infants would either sit down or else walk forward, carrying the other monkey with them and sometimes falling off the branch as a result. Only once did the monkey being mounted, an adult female, remain still throughout. Fig. 7.2 gives an example of the sort of imperfect posture achieved by young animals. In this case a juvenile seized an adult that was walking past and tried to mount, but though it managed to grip the adult's hind legs with its feet it was only able to take hold of the fur on its rump rather than further up the back as is normal. It was hence unable to bring its genital region into contact with the adult's. In some cases sheer

size differences made normal mounting impracticable. For instance a large juvenile was unable to mount a small infant, but instead took hold of its body just in front of the hindlimbs, pulled it up against its genital region and made pelvic thrusts, and then released it.

Days on which mounting was observed are shown in fig. 7.3. Mountings of females by mature or young males are distinguished from those involving young animals. Mountings of the former type appear to have been concentrated in September and October during 1966, but this is probably purely fortuitous and the numbers involved are too small to draw any conclusions as to seasonality of copulation. If females show cyclic changes in receptivity, and one female happened to be in oestrous at a time when its group was readily observable, an artificial concentration of records could result. Two mountings on 29/9/66 were of the same female in group A by the same male, within 20 minutes of one another. Likewise the mature male in group B mounted the same female on 4/10/66 and 6/10/66, and possibly on 5/10/66 as well.

Female Cercopithecus monkeys do not show any obvious external signs of oestrous. In this respect they differ from monkeys such as the talapoin and the

FIG.7.3 DISTRIBUTION OF MOUNTING OVER THE YEAR

KEY: I.... Mountings of adults by adults, o....other mountings.
Study periods underlined.

FIG.7.4 DISTRIBUTION OF BIRTHS OVER THE YEAR

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1965							....ACC....					C
1966	CA					ABA		C	D		B	
1967	DD	CC										

Letters refer to groups in which babies were born.

baboon/macaque group, in which cyclic changes in the sexual skin may be observed. It is hence impossible to tell, in the field, whether or not females are potentially receptive. However, as Rowell (1966a) and Kummer (1968) point out, females probably spend most of their time pregnant or lactating rather than cycling, so in a small group there might be long periods when no females were receptive.

BREEDING.

When the study area was first visited in late August and early September 1965 three babies were seen, one in the region subsequently found to be group A's range and two in group C's. Their dates of birth are uncertain, but would have been some time in July or August.

At least 13 babies were born in the study area between August 1965 and March 1967. A baby was seen in group C's range in late December 1965, which judging by its size would have been born about the beginning of the month. At the same time a clearly pregnant female was observed in the same group's range, and from Jan. 13th onwards a very small baby was seen. This would therefore have been born in early January. The two babies were sometimes

observed in the same party, and could be distinguished by differences in size and colouration until they reached the infant stage.

During this period a baby was born also in group A. It was first seen on Feb. 17th, and was similar in size to the younger of the two babies in group C. It too would hence have been born in early January.

I was unable to be in Budongo between late April and early June 1966. During my absence three more babies were born, two in group A and one in group B. The latter was first seen on June 4th, and would probably have been born about mid May. The two babies in group A were first seen on June 11th. One, belonging to a recognisable female, was small, perhaps two weeks old, and the other noticeably larger, maybe a month old. The first of these subsequently disappeared. It was seen regularly up to July 27th, but thereafter its mother was seen several times apparently alone. The remaining baby continued to be seen at regular intervals until it had grown to infant size.

On July 23rd a very small baby, less than a fortnight old, was seen in group C's range. It was observed only on this one occasion, but as group C was not contacted very often during August and

September this does not necessarily mean that it had disappeared.

Likewise on August 8th a baby only two or three days old was seen in group D, but was observed only once thereafter, on Sept. 9th.

A further baby was born in group B at the end of September. It was first seen on Oct. 2nd, when still very small and certainly less than two weeks old, and was observed thereafter at regular intervals until the end of the study in March 1967.

On Jan. 23rd 1967 a female in group D was seen carrying one baby, perhaps three weeks old, with a second baby running along unsteadily behind her. No other females were visible in the immediate vicinity, and the second baby was too small to move far from its mother. It is possible that the two babies might have been twins; Osman Hill (1966) records four cases of twins in Cercopithecus spp. However, a female, probably the same one, was seen with only a single baby in the same area five days later and twice thereafter during the next month, so the second baby apparently disappeared.

On Feb. 9th two further babies were seen in group C. One was very small, with noticeably pink ears, and so could have been only a few days old.

The other was slightly larger and had grey ears, and would hence have been born some time in late January. Both these babies were seen on subsequent occasions up to the end of the study.

In addition to these recorded births, a clearly pregnant female was seen in group A on three occasions at the end of January 1967.

The distribution of births over the year is summarised in fig. 7.4. Births are recorded for all months apart from March, April, October and November. Clearly, therefore, there is no discrete birth season, but the possibility of a birth peak or peaks cannot be ruled out. While the numbers involved are too small for any hard and fast conclusions to be drawn, there is some suggestion of a concentration of births during the dry season of December, January and early February, and perhaps another concentration between May and September.

Booth (1962) found that for monkeys of the C.mitis group in Kenya there was a definite concentration of births at one time of year in areas where food availability fluctuated considerably from season to season. The timing of this birth peak varied from one locality to another. In captivity, on the other hand, with a regular food supply, births

were distributed throughout the year. In contrast captive C.albegularis at Makerere showed a tendency for births to be concentrated in the two dry seasons, that is Dec./Jan. and June/July, with gestation of around 140 days (Rowell, pers.comm.).

For C.ascanius Haddow (1952) collected evidence suggesting that there is at least a preferential breeding season. In a sample of 52 females, shot at all times of the year, early pregnancies were most frequent from January to April, late pregnancies from May to September, and infants (referring in this case to monkeys less than 6 months old) from September to April. In contrast a sample of Colobus guereza of similar size showed no such season variation. Haddow suggests that this may be related to differences in diet, colobus being leaf eating and hence having a relatively constant food supply while redtails are largely frugivorous and therefore perhaps more subject to fluctuations in the availability of food.

Gartlan (1966) found that a population of C.aethiops on Lolui Island had a distinct birth season from mid April to mid September. The season started in the middle of the rains and may thus be functionally related to changes in the availability of food.

Seasonality of breeding in primates has been discussed by Lancaster and Lee (1965). They concluded that a birth peak, if not a birth season, was present in most populations for which detailed data were available. The proximal determination of seasonality appeared to be related to such factors as changes in day length, high rainfall and favourable diet, though as Sugiyama's (1965c, 1966) observations on Presbytis entellus show, social factors may play some role as well. The ultimate causation or function of seasonality in breeding is presumably to ensure that the reproductive cycle is favourably related to environmental changes. This does not necessarily mean that the young are born at times when food is most abundant; in some species other parts of the cycle such as pregnancy or weaning fall at this time.

The lack of a restricted birth season in the blue monkey could be related to the apparent absence of pronounced seasonal changes in the availability of food. Food supplies fluctuate considerably, but change from week to week rather than from season to season. Comparison with baboons may be instructive here; populations in southern Africa do not have a clear cut concentration of births at

any one time of year, whereas those in East Africa, where seasonal changes in their habitat are more pronounced, do. A similar contrast exists between populations of langurs in moist deciduous forest and ones in regions where the dry season is more pronounced (Yoshiba 1968).

MATERNAL BEHAVIOUR AND INFANT DEVELOPMENT.

Only 7 of the 13 babies were positively identified on more than 5 occasions, and since females with babies tended to be wilder than other members of the group they could seldom be kept under observation for more than a few minutes. Detailed quantitative study of changes in the young monkey's relations with its mother was therefore impracticable; one has to be content with piecing together an outline of development from fragmentary observations. In view of the restricted data available and the chance of errors in the estimation of putative dates of birth the timing of the events outlined below should be considered merely approximate.

Initially babies cling to their mothers the whole time and are carried everywhere by them. The baby hangs below the mother's body, holding on to the fur on her sides with its hands and feet (see fig. 7.5).

FIG.7.5 A female carrying a week-old baby.

FIG.7.6 A female leaping from one tree to another with her baby clinging beneath.

One nipple is held in the mouth. The tail is prehensile at this age, and may be hooked over or coiled round the base of the mother's. Young monkeys are capable of supporting themselves in this position almost immediately after birth (Booth 1962), and remain firmly attached even when the female is moving rapidly or leaping from tree to tree (see fig. 7.6). The same grip is maintained when the female is sitting. Females with small babies tend to assume a more hunched posture than the normal sitting position, and the legs may be stretched out forwards.

Between 10 and 14 days after birth the baby may climb down off the female and sit between her legs. The mother restrains it if it attempts to move out of reach, usually keeping a hold on its tail and pulling it back if it moves as much as an arm's length from her. The baby is unsteady on its feet at this age, and liable to stumble and slip.

By three to four weeks of age the baby is more coordinated in its movements and the mother does not restrain it if it attempts to move out of her reach. It seldom goes more than a few feet away, though, and she at once seizes it and pulls it in to her body if anything alarms or startles her. For instance

females would often pick up babies of this age and move off with them when they saw me looking at them.

By the time it is five or six weeks old the baby is quite agile. Less time is spent in contact with the mother and it may move as much as 30 - 40 ft. from her. It bounces around in the branches, pulls at leaves, and chews twigs, but as far as can be seen does not actually eat anything. When in contact with the mother it may sit beside her rather than clinging to her front. However it runs to the mother and clings to her when frightened, and is carried whenever she moves; if she stands up and walks a few feet the baby runs back to her, whereupon she puts a hand on its shoulder and pulls it in to her and it clings on beneath.

At 1½ to 2 months the baby begins to move independently of its mother, but it is still carried when the group is moving fast or over difficult places. At this age it begins to eat solid food such as leaves and buds, and may actively solicit grooming from its mother.

By 2½ months the young animal usually moves independently and is thereafter classified as an infant rather than a baby. Infants are occasionally carried after this age; one infant was seen carried

when over 5 months old and so large that the female was unable to walk normally, but such behaviour was exceptional.

At around 2½ months the young animal starts to have social contacts with monkeys other than its mother, and these become progressively more frequent. However, links with the mother are still maintained; infants sit with females more than they do with other classes, for example, and are more likely to be involved in grooming interactions with them. These links may not be broken until the birth of the next baby; an infant was once seen to try to suckle from a clearly pregnant female. The female resisted its initial attempts to take a nipple in its mouth, but finally allowed it to do so for half a minute before pushing it off.

The general outline of development is thus similar to that in many other species. The only other Cercopithecus sp. for which detailed information is available is the vervet (Gartlan 1966). Young vervets appear to develop rather more rapidly than blue monkeys during the first 2 - 3 months, but this apparent contrast may result from the small amount of data available in the present study rather than from any genuine differences in behaviour.

A marked contrast between the blue monkey and certain other species lies in the behaviour of other members of the group to the baby and its mother. In many species mothers with babies are a centre of attraction among other members of the group, and in some the baby may be handed around, or carried by monkeys other than the mother. For example baby langurs are regularly handled by females other than the mother within a few hours of birth (Jay 1965), and in the Barbary macaque females with babies attract attention from other members of the group and the young are frequently carried by adult males and by juveniles of both sexes within days of birth (Deag, pers.comm.). In C.aethiops other females, particularly subadults, take a keen interest in the young infant and attempt to take it from the mother, and she may allow them to remove it and carry it within a few days of its birth. By 2 months of age the young vervet monkey spends more than 25% of its time in tactile or social contact with animals other than the mother (Gartlan 1966).

In the blue monkey, on the other hand, females with babies do not appear to act as a focus of attention, and a baby was never seen to be carried by any monkey positively identified as being other

than its mother. Indeed it seems that females with babies may be involved in rather fewer interactions than other females. For example females with babies were seen to sit with other animals on five occasions, whereas other females were seen to do so 222 times. Using the methods developed in the previous chapter, it can be shown that females with babies would be expected to participate in 22.05% of the interactions involving females, giving an expected value of 50.1. Observed values for sitting associations differ significantly from the expected values (X^2 = 52.10 with 1 d.f. p =<0.001). In practice the discrepancy may be greater than the figures imply, since no account is taken of interactions involving unsexed adults. These would involve many females, but few if any females with babies.

It could be argued that to compare associations between the two categories of females and all other classes is misleading, since many of those involving females without babies will be female/infant associations. Even if the latter are excluded, though, the discrepancy remains:

	Females with babies	Other females
Observed	3	113
Expected	25.6	90.4

X^2 is 25.60 with one degree of freedom, for which p =<0.001.

In species exhibiting 'aunt' behaviour other monkeys may attempt to make contact with the baby by first grooming its mother. For instance Gartlan (1966) describes how other vervets usually approach the mother in the first instance and groom her, gradually working closer to the infant, rather than trying to handle or remove it directly. Were comparable behaviour found in the blue monkey one would expect females with babies to be involved in relatively more grooming interactions than other females. In fact the reverse appears to be true; females with babies were involved in 9 grooming interactions and other females in 218, as against expected values of 50.1 and 176.9. X^2 is 43.27 with one degree of freedom, for which p =<0.001. The discrepancy persists even when interactions involving infants are excluded:

	Females with babies	Other females
Observed	8	172
Expected	39.7	140.3

X^2 is 32.47 with one degree of freedom, for which p =<0.001.

The low numbers of interactions involving females with babies appear to be the result of lack of interest by other animals as much as of avoidance on

the part of the mother. Other monkeys were seen to approach females with babies only 6 times, as against 126 for other females. Expected values, were both categories of female approached at random, are 29.1 and 102.9 respectively. X^2 is 23.52 with one degree of freedom, for which p =<0.001. If approaches by infants are excluded, the figures are as follows:

	Females with babies	Other females
Observed	5	68
Expected	16.1	56.9

X^2 is 9.818 with one degree of freedom, for which p =<0.01. It would appear, therefore, that females with babies are somewhat less likely to be approached than are other females.

Taken at face value, the data above indicate that not only do other monkeys take little interest in females with babies, but that they are much less likely to interact with them than with other females. The latter conclusion could in part, however, be a result of the greater shyness of females with babies, which would reduce the chances of observing such interactions as they participated in, rather than of a reluctance to interact with other monkeys. Females with babies did sometimes appear to keep on the edge of the party that they were in, but in such cases at

the edge furthest from the observer. When females with babies that were more tolerant of my presence were observed, they appeared neither to avoid nor to associate closely with other monkeys.

PLAY.

At between 2½ and 3 months of age infants start to become involved in social play interactions. Play is commonly initiated by one animal approaching another and 'sparring' at it, that is, standing on the hind legs and striking towards it with the fore-limbs. A characteristic facial expression, with the mouth open exposing the teeth, is generally assumed by the animal inviting play. A comparable expression, presumably the equivalent of the 'relaxed open mouth face' described by Van Hoof (1967) in his review of primate facial expressions, is seen before and during play in many other primates. Alternatively play may be initiated by one monkey pulling another's tail, or simply by jumping on top of the other animal. In captive C.albogularis at Bristol play was sometimes initiated by a 'bouncing' movement, in which the body was jerked up and down while the hands and feet remained on the substrate. This type of invitation was seen only once in the wild, given by an infant to a female. In C.aethiops a similar movement appears

to serve as a threat (Struhsaker 1967b).

If, as is usually the case, an invitation to play is accepted, three types of play may follow ... chasing, sparring, and wrestling. In chasing, the two animals rush along branches and round tree trunks a few feet apart, with the lead alternating from one to another. Such chases may be distinguished from aggressive chases (see p. 312) by virtue of this rapid reversal of the roles of chaser and chased, and by their close association with other play patterns. In addition play chases may continue, perhaps intermittently, for much longer than aggressive chases.

In sparring, the two monkeys stand on their hind legs, facing one another and making the 'play face' described above, and strike towards one another. If contact is made at all, it is no more than hand to hand. In wrestling, they close and grapple with one another at close quarters. Each participant takes hold of the other, usually by the shoulders, and pushes it and bites at its head, shoulders and forelimbs. Biting during play is distinct from biting under aggressive circumstances, (as observed in captivity), in that the mouth is not closed far enough for the teeth to exert much pressure. Bouts of wrestling commonly end by one animal being pushed

off the branch and falling into the foliage below. As a rule this terminates the session, though monkeys would sometimes climb up again and resume playing. All three types of play may alternate and merge into one another. On four occasions mounting was seen during play sessions.

The main features of blue monkey play are common to most other Old World species, but many of these show further and more elaborate patterns not seen in C.mitis. For example in C.aethiops Gartlan (1966) describes a pattern referred to as 'chain jumping', in which infants leap in procession from a low branch to the ground and then climb up again and repeat the manoeuvre, sometimes as many as five times. Another difference that may be significant is that young blue monkeys were seldom seen to indulge in non-social play with inanimate objects, while such behaviour is frequent in some other species. Young baboons in Budongo, for example, spent much time swinging on lianas.

Bouts of play were usually short; the mean length of 40 bouts was 43 secs, and none lasted for more than 2½ minutes. This again provides a contrast with some other species. In Erythrocebus patas, for example, play sessions may last as long

as half an hour (Hall 1965), and in C.aethiops mean duration of infant/infant social contacts rose from over a minute at age 2 months to nearly 4 minutes at 5 months (Gartlan 1966).

Fifty five social play interactions were recorded. This total includes six complex interactions involving three monkeys, split into the appropriate dyads. The distribution of these interactions among the various sex and age classes is shown in fig. 7.7. It will be noted that 49 of the 55 interactions involve infants, 30 being infant/infant interactions.

The not unexpected impression that infants play more than other classes is confirmed by statistical analysis. Comparison of observed and expected values for participation in play interactions, (the marginal totals in fig. 7.7), yields a X^2 of 75.16 with 4 degrees of freedom, for which $p =< 0.001$. Nearly half this value is contributed by the discrepancy between observed and expected values for infants.

Given that infants play more than other classes, it can be shown that their partners in interaction are not drawn at random from the population; they play more with members of their own class than with other classes. The table below shows the number of times

FIG.7.7 Frequency of play interactions between the various classes.
(Expected values in brackets)

♀ \ ♂	mature male	young male	female	unsexed adult	juvenile	infant	baby	TOTAL
mature male	-	-	-	-	-	-	-	- (9.4)
young male	-	-	-	-	-	-	-	- (10.5)
female	-	-	-	-	-	3	-	3 (34.5)
unsexed adult	-	-	-	-	2	4	-	6
juvenile	-	-	-	2	2	12	-	17* (16.4)
infant	-	-	3	4	12	30	-	49 (21.4)
baby	-	-	-	-	-	-	1	1 (8.0)

*Juvenile total includes one interaction with an unclassified animal, probably an infant or another juvenile.

that infants played with members of each class, together with expected values, calculated from the probabilities in fig. 6.3, were association random.

	MM	YM	F	UA	J	I	B	T
observed	-	-	3	4	12	30	-	49
expected	4.6	5.1	19.8		8.3	74	3.7	48.9

Combining adults other than mature males into a single category, and infants and babies into another so as to eliminate the low expected value for the latter class, X^2 is 51.3 with 3 degrees of freedom, for which $p =< 0.001$.

AGONISTIC BEHAVIOUR AND INDIVIDUAL SPACING.

Agonistic behaviour patterns form a continuum from mild threat on the one hand to actual attack on the other. For descriptive convenience they may be separated into the categories below. Since agonistic interactions were observed but rarely in the wild, the finer details are based on observation of captive animals.

(i) Threat. The monkey stares directly at the animal being threatened, with eyebrows raised. The mouth may be closed, or at higher intensities slightly open but without revealing the teeth (see

fig. 7.8). If the monkey is sitting it may lower the head and thrust it forward, or if standing flex the forelimbs and perhaps make a short lunge towards the other animal.

(ii) Rum at. One monkey rushes at the other. In some instances the head is held low and the tail straight out behind, but the degree to which such a posture is assumed varies. Grating calls (see p.197) may be given. When such behaviour precipitates a chase it is usually short.

(iii) Grapple and bite. One animal seizes the other with both hands and bites any available part of its anatomy. Actual biting was seen only once in the wild. On the other hand it was common in captivity, particularly when monkeys had just been introduced into the group; indeed some individuals were so severely bitten that they had to be removed.

(iv) Hit. One monkey strikes the other, with the hand open. The movement is similar to play sparring, but is performed with greater vigour and usually as a single blow rather than the repetitive blows of sparring. Hitting does not lie so clearly on a continuum of behaviour as the three previous patterns; whereas these might follow one another in

FIG.7.8 A juvenile Sykes' monkey threatening the camera. Note the raised eyebrows and slightly open mouth.

succession hitting was generally seen in isolation.

All these behaviour patterns have parallels in other species. For instance the facial expression assumed during threat presumably corresponds to the 'staring open mouth face' of Van Hoof (1967), variants of which are common to most Old World monkeys. The raising of the eyebrows, though, is far less marked than in animals such as baboons; indeed this expression provides a good example of the relative immobility of the facial musculature of C.mitis as compared to that of other species, particularly those living in open conditions. In addition blue monkeys lack contrastingly coloured regions of the face to accentuate the expression; in baboons the raising of the eyebrows is emphasised by the paler skin around the eyes, and the same is true of C.aethiops. (See Gartlan and Brain 1968 for photos comparing threat expressions in the two Cercopithecus spp.).

While all these behaviour patterns are seen in other species as well, some monkeys, particularly terrestrial species, have a much more varied repertoire. For instance both Gartlan (1966) and Struhsaker (1967b) describe various forms of 'head jerking' or 'bob and bounce' threat in the vervet that

were not seen at all in wild C.mitis and only seldom in captive animals. As yet we lack sufficient information on other forest Cercopithecus spp to decide whether the repertoire of C.aethiops has become more elaborate than that of typical forest species as a response to the more open habitat. Head jerking, for instance, was a common reaction to the observer among C.aethiops in Budongo (cf. also Haddow 1952). Moreover the relative frequency of behaviour patterns and the circumstances in which they are seen may be of greater significance in interspecific comparisons than mere size of the repertoire.

In the wild other monkeys usually responded to threats simply with avoidance. Threats were seldom returned except during intergroup encounters. Likewise the usual response to being run at was simply to flee, perhaps giving chatters (see p.199). In captivity, on the other hand, no such ready means of escape is available since the monkeys can never get more than a few feet away from one another. Hence incidents that in the wild would involve only threat and avoidance may in captivity lead to a fight.

Only 29 instances of threat and aggression between members of the same group were observed.

Fig. 7.9 shows the distribution of these incidents among the various classes. The number of interactions is too low to determine whether individual classes were aggressors or victims of aggression more or less often than would be expected. The data suggest, though, that adults as a whole were more likely to be aggressors than were young animals. Thus adults were the aggressors in 21 of the 28 interactions involving classified animals, as against 7 for young animals. Expected values, were interaction random, are 15.71 and 12.29 respectively. X^2 is 4.057 with one degree of freedom, for which $p =< 0.05$. No such difference can be shown as regards the victims of aggression (X^2 = 1.995 with 1 d.f.).

As mentioned above, in only one of these 29 interactions was any animal bitten; indeed physical contact was usually limited to a single blow. Four of the interactions involved threat only. Aggressive chases were seen 11 times, and were twice followed by threat. One monkey was seen to hit another on 13 occasions; in three of these instances striking was associated with chasing but in the remainder it was not accompanied by any other aggressive behaviour. Vigorous wrestling and grappling was observed on five occasions.

FIG.7.9 Frequency of aggressive interactions between the various classes.

Aggressor:	mature male	young male	female	unsexed adult	juvenile	infant	baby	other	TOTAL
mature male	-	-	-	1	-	1	-	-	2
young male	-	-	-	-	-	-	-	-	-
female	-	-	3	-	3	1	-	-	7
unsexed adult	-	-	1	7	2	2	-	-	12
juvenile	-	-	-	-	3	2	-	-	5
infant	-	-	-	-	-	2	-	-	2
baby	-	-	-	-	-	-	-	-	-
Other	-	-	-	-	-	-	-	1	1
TOTAL	-	-	4	8	8	8	-	1	29

The circumstances under which aggressive interactions occurred were determined in 21 cases. Eight took place while monkeys were feeding, but in none of these did the incident appear to be precipitated by competition for an individual food item. On the contrary, most happened in trees such as fruiting Celtis or Ficus spp bearing a heavy crop of fruit, and were initiated by one monkey running at another from several feet away. All but one of such interactions were between members of the same class.

The remaining interactions took place under a diversity of circumstances. In four cases one animal struck at another when it apparently tried to play, and in another two infants were hit when they persistently solicited grooming. In two instances adults ran at other monkeys that were playing roughly with or persistently soliciting grooming from infants. Other incidents included a mature male threatening an adult that had been 'harassing' it during copulation, a female striking a juvenile that attempted to mount it, and an adult striking an infant that fell on top of it after being dislodged from a branch above during play.

It is clear that agonistic interactions play

little part in the day to day behaviour of the blue monkey. Twenty nine interactions in 450 hours of observation gives a frequency of 0.06 interactions per hour, or one every 15.5 hours. Even if the 10 or so interactions that were heard but not seen are included, the frequency only rises to one every 11.25 hours or 0.09 per hour. Hall (1965) recorded 49 aggressive interactions in 627 hours observation on the patas monkey (0.08/hr.), as against 167 such interactions in 190 hours observation of a group of baboons at the Cape (0.88/hr.). During 1472 hours of observation on C.aethiops Gartlan (1966) recorded 423 aggressive incidents (0.29/hr). For the black mangabey Chalmers (1967) found that the numbers of aggressive encounters varied greatly with feeding conditions; during 25 hours when the monkeys were feeding on localised fruits 112 agonistic encounters were seen (4.48/hr.), but this fell to only 10 (0.40/hr.) when they were feeding on the more typical dispersed fruits. Overall frequencies for two groups were 1.26 and 1.07/hr.

These figures suggest that blue monkeys are less aggressive than most other species. Direct comparison of figures should be made with caution, however. Conditions of observation are far better

in open country, and in many cases groups are larger; hence more interactions are likely to occur within the group and such as do take place are more likely to be seen. Comparison of numbers of incidents per 'monkey observation hour' rather than 'man observation hour' would go some way towards alleviating this difficulty, but accurate information is seldom available in such a form. In addition the types of interaction classified as agonistic may differ from one observer to another. Nevertheless the apparent contrasts between species are in some cases so striking that they seem unlikely to be wholly artificial. The apparent rate for the Cape baboons is ten times that for the blue monkey, and for mangabeys, living in a similar habitat to blues, at least 12 times.

Perhaps of greater significance are the contrasts in classes of animals involved in agonistic interactions and the context within which such behaviour is seen. In Papio hamadryas, for instance, adult males frequently threaten or even attack females of their own 'one male group' if they stray more than a few yards from their leader (Kummer 1968). Likewise in Theropithecus gelada adult males, though permitting their females to move much further away

than is the case in the hamadryas, periodically regain contact with them by chasing them (Crook, pers.comm.). In savanna-living baboons aggression on the part of the adult males sometimes appears to break up squabbles between other members of the group, protecting mothers and infants from injury, or to increase group cohesion in the face of external disturbance (Hall and DeVore 1965). In all these species, therefore, aggressive behaviour by a particular class of animal appears to be of functional significance in the maintenance of group structure. In the blue monkey there is no tendency for mature males, or for that matter any other class, to behave in such a way. Many of the few aggressive incidents that were seen could almost be described as accidental: (for instance cases in which vigorous play invitations were apparently 'misunderstood' and met with aggression, and instances in which one animal suddenly jumped up beside or fell on another). Gartlan (1966) makes a similar point regarding intra-group aggression in C.aethiops; many aggressive incidents were precipitated by the breakdown of the normal 'social monitoring' mechanisms.

Not only are blue monkeys seldom involved in overt aggressive behaviour, but they also lack many of

the more subtle manifestations of tension or hierarchical relationships between individuals to be seen in other species. For instance many interactions that do not involve overt threat or aggression can broadly be classified as 'approach-retreat' interactions.. These may involve supplanting of one animal by another at a food source, grooming partner, or other desirable object, or merely priority in the use of space. In groups that can be described as having a hierarchical organisation low ranking animals continuously 'monitor' the position of higher ranking ones, and may turn aside or move away if the latter approach them (see, for example, Rowell 1966b, 1967, Struhsaker 1967a, Gartlan 1966). Indeed Chance (1967) regards this 'attention structure' as being a critical determinant of social organisation.

In the blue monkey, clear cut supplanting was virtually never seen, and few if any interactions other than those involving overt threat or aggression could be fitted into an approach-retreat pattern. Moreover approach-retreat interactions were seen not to take place under many of the circumstances in which they might be expected. For example it was commonplace for one monkey to walk past or jump over another on the same branch without either animal

showing signs of avoidance, or behaviour such as urination or scratching that could be considered as indicative of nervousness. In only 5 cases was one monkey seen to move out of the way of another, and in one further case a monkey scratched itself as another squeezed past on the same branch. Thus there is little if any conflict over space as such. In contrast Struhsaker (1967a) found that in groups of C.aethiops with a marked hierarchical structure space was apparently the focus of most of the supplanting.

Likewise 'social monitoring', watchful glances by some monkeys apparently to keep track of the location and behaviour of others, was not evident in the blue monkey. Admittedly such behaviour would be easy to overlook under forest conditions; mere eye movements as against turning of the head would almost certainly be undetected. On the other hand social monitoring WAS apparent in forest baboons in the study area, so it seems safe to conclude that it is not very frequent in the blue monkey. Since the group is usually widely dispersed one would anyway not expect to see such behaviour very often.

In many species, particularly those in which a hierarchical structure has been described, the social

relations between individuals or classes are reflected in their spatial distribution within the group. For instance in provisionised Japanese macaque troops peripheral males are peripheral in both a social and a spatial sense (Imanishi 1963). Likewise in baboon troops moving across open savanna dominant males occupy the centre of the troop together with females and young, and subordinate males are distributed around the edge (Hall and DeVore 1965, but see Rowell 1969 for an alternative picture of baboon troop movement). In the blue monkey no clear cut spatial organisation could be detected. In particular the mature male appeared sometimes to be in the centre of the group and at other times right on the edge. Since groups were typically widely scattered, and only a small part of the group visible at any one moment, such relationships would be difficult to detect. I gained the impression, though, that their apparent absence was genuine rather than an artifact of the observational conditions.

Similarly no single individual or class of animal appeared to 'lead' the group or party, or to initiate movements. Organised movements of the whole group were rare, and even smaller parties

seldom moved in an integrated fashion. The typical mode of progression was a gradual drift, individual animals moving a short way and then pausing awhile to sit or feed, when others might move past them. Thus even if the whole party followed the same route through the canopy the order of progress would change frequently. In the few cases in which the order remained relatively constant there was no tendency for the apparent 'leader' to belong to any one class.

The animals in the van of a group movement do not necessarily determine the direction of movement; this may be influenced by monkeys in the centre of the group. For instance in Papio hamadryas two male teams, associations of two one male units, often move together. Movements are generally initiated by the younger of the two males, but the party as a whole does not follow unless the older male at the back is prepared to do so (Kummer 1968). In the blue monkey no individual appears to have any regular influence on the direction of movement. For instance on one occasion a mature male that had been sitting inactive in the middle of a foraging party suddenly stood up and moved off, whereupon the rest of the party began to drift away in the same direction. On another occasion, however, a similar party moved off leaving the mature male behind; 15 minutes later when they were about 150 yards away he suddenly sat up, looked around, and ran off after them.

ASSOCIATIONS BETWEEN THE VARIOUS CLASSES.

The nature of the bonds between classes or individuals may be inferred firstly from the type and frequency of social interactions between them, and secondly from their spatial relations. In other field studies systematic data on 'nearest neighbours' has been collected. Kummer (1968), for instance, collected such data by picking a subject animal at random and recording the identity of the three animals nearest to it, and a similar approach was adopted by Deag (pers.comm.) in his study of the Barbary macaque. Conversely Gartlan (1966) systematically recorded instances of animals more than 10 metres from their nearest neighbour, so as to determine whether any age sex class was habitually found away from other animals. Such methods are inappropriate under forest conditions, since the true nearest neighbours may be obscured by foliage and the various classes may differ in their likelihood of being so concealed. In the present study, therefore, records were taken only of monkeys that were actually sitting together, that is in contact or within arms reach of one another.

Monkeys were seen sitting together, without overt social interaction other than mouthing when one animal approached another, on 283 occasions. The

distribution of these associations among the various classes is given in fig. 7.10. In a further 250 cases animals were either sitting together for at least a minute before or remained together after social interactions, mainly grooming interactions. The distribution of such associations is shown in fig. 7.11.

Comparison of the marginal totals of the two figures yields a X^2 of 70.26 with 4 degrees of freedom, (adults other than mature males being treated as a single category), for which $p =<0.001$. Hence the likelihood of the various classes being involved in sitting associations differed in the two situations. In particular, babies were more likely than were other classes to sit with other animals without interaction.

Comparison of the observed marginal totals in fig. 7.10 with expected values, calculated from the probabilities in fig. 6.1 as proportions of 283, gives a X^2 of 145.16 with 4 degrees of freedom (young males, females and unsexed adults being combined) for which $p =<0.001$. Hence the involvement of the various classes in sitting associations in the absence of interaction differed from what would be expected were association random. Babies, adults other than mature males, and to a lesser extent

FIG.7.10 Numbers of times the various classes were seen to sit together without overt interaction. (Expected values in brackets)

	mature male	young male	female	unsexed adult	juvenile	infant	baby	TOTAL
mature male	-	-	5	3	-	-	-	8 (48.5)
young male	-	-	-	-	-	2	-	2 (54.0)
female	5	-	2	8	9	67	89	180 (177.7)
unsexed adult	3	-	8	17	10	48	3	89
juvenile	-	-	9	10	1	10	-	30 (84.6)
infant	-	2	67	48	10	9	-	136 (110.3)
baby	-	-	89	3	-	-	-	92 (41.0)

FIG.7.11 Numbers of times the various classes were seen to sit together before or after interacting. (Expected values in brackets)

	mature male	young male	female	unsexed adult	juvenile	infant	baby	TOTAL
mature male	-	3	7	8	2	1	-	21 (42.8)
young male	3	-	3	1	2	1	-	10 (47.7)
female	7	3	13	36	15	43	9	126 (157.0)
unsexed adult	8	1	36	32	18	27	2	124
juvenile	2	2	15	18	4	5	-	46 (74.8)
infant	1	1	43	27	5	18	-	95 (97.4)
baby	-	-	9	2	-	-	-	11 (36.3)

infants sat with other monkeys more than expected, and mature males and juveniles less.

Analysis of the 92 associations involving babies shows that this excess of sitting was not distributed at random among the classes; indeed all but three were female/baby associations. Observed and expected values, calculated as proportions of 92 from the probabilities in fig. 6.3, are as follows:

	MM	YM	F	UA	J	I	B	T
observed	-	-	89	3	-	-	-	92
expected	7.1	10.7	36.5		14.2	21.3	2.2	92

Combining young males, females, and unsexed adults, X^2 is 87.32 with 4 degrees of freedom, for which $p =< 0.001$.

While infants were more catholic in their choice of partner, they too did not associate at random with all other classes. Observed and expected values, calculated on the same basis as above, are as follows:

	MM	YM	F	UA	J	I	B	T
observed	-	2	67	48	10	9	-	136
expected	12.7	14.2	55.1		23.0	20.6	10.3	135.9

Combining young males, females, and unsexed adults into a single category, X^2 is 69.71 with 4 degrees of freedom, for which $p =< 0.001$. Thus infants sat with adults other than mature males more often than expected, and with other classes less.

Comparison of the observed marginal totals in fig. 7.11 with expected values, calculated as proportions of 250 from the probabilities in fig. 6.1, yields a X^2 of 54.83 with 4 degrees of freedom (combining adults other than mature males as before), for which $p =< 0.001$. Hence in this situation also the involvement of the various classes in sitting associations differs from what would be expected were association random. Mature males, juveniles, and babies sat with other animals less than expected, and adults other than mature males more. Note, however, that this pattern differs in certain respects from that shown in fig. 7.10; in particular babies sat with other animals less than expected in the present case, but more than expected in the absence of overt interaction.

In 78 of the 283 associations not involving behaviour such as grooming one animal was seen to approach the other and sit by it. Fig. 7.12 gives the number of times the various classes were seen to approach one another. Forty six of the 78 approaches were made by infants to adults other than mature males, 34 of these being identified as females. The impression that infants are more likely to approach than are other classes, and adults other than mature males more likely to be approached, is confirmed by

FIG.7.12 Numbers of times the various classes were seen to approach one another prior to sitting together. (Expected values in brackets).

Class approached: / Class approaching:	mature male	young male	female	unsexed adult	juvenile	infant	baby	TOTAL
mature male	-	-	-	-	-	-	-	- (6.9)
young male	-	-	-	-	-	-	-	- (7.5)
female	4	-	-	1	-	2	1	8 (29.4)
unsexed adult	1	-	1	3	1	1	-	7
juvenile	-	-	5	2	-	1	-	8 (12.3)
infant	-	1	34	11	1	1	-	48 (16.5)
baby	-	-	5	2	-	-	-	7 (5.5)
TOTAL	5 (6.9)	1 (7.5)	45 (29.4)	19	2 (12.3)	5 (16.5)	1 (5.5)	78

statistical analysis. Thus comparison of observed and expected values (calculated from the marginal probabilities in fig. 6.2) for the total number of approaches made by each class yields a X^2 of 72.79 with 4 degrees of freedom, for which $p =< 0.001$, 60.14 of this value being contributed by the discrepancy between observed and expected values for infants. Likewise comparison of observed and expected totals for the number of times each class was approached gives a X^2 of 42.24 with 4 degrees of freedom, ($p =< 0.001$), half of which originates in the figures for unsexed adults. Moreover the observed value for approaches to females is substantially higher than the expected value even without possible inclusion of unsexed adults; if unsexed adults are excluded from the calculation and females and subadult males treated as separate categories the result is still significant ($X^2 =$ 34.76 with 5 d.f. $p =< 0.001$). That infants approach females rather than females approaching infants suggests that the initiative in maintaining association with its mother lies largely with the young animal at this stage in its development.

These findings may be contrasted with the pattern of approaches prior to grooming interactions

(see p.252). It will be recalled that while adults other than mature males were more likely to be approached, no single class was more likely to approach than any other.

INTERGROUP RELATIONS, AND SOLITARY MALES.

Typical agonistic intergroup encounters have already been described in Chapter 2. Such encounters are characterised by the giving of volley calls and 'bouncing' displays ... conspicuous bounding from branch to branch ... by the mature male in each group, and by threats and chases between other animals. Groups tend to be more compact during intergroup encounters than at other times.

Fourteen clear cut agonistic encounters between groups were observed. Nine of these, spread over a period of 5 days, were between groups E and F, and took place in a fruiting Aningeria altissima in the overlap zone between their ranges. The overall outcome of these encounters was inconclusive; in some cases one, in some the other, and in some both groups withdrew. A further three incidents occurred when group C intruded into group A's range to feed in fruiting Pseudospondias trees; in all of these group C was driven out again. The remaining two incidents involved groups B and D, and were not

related to any obvious food source. In both group D apparently intruded into group B's range, and subsequently withdrew. The locations of these encounters have already been given, in fig. 2.11.

Agonistic encounters occurred only when one group moved outside its normal range, or when two groups were actually feeding in the same trees. At other times members of different groups appeared to tolerate one another at comparatively close quarters, though perhaps with watchful behaviour on the part of the mature males.

For example, on the morning of 15/2/67 parties from groups C and D were feeding 100 yards apart, on the edges of their ranges. The mature male from group D appeared, looked across to group C, and bounded towards it for 50 yards. As it did so there were chirps and sudden movements from group C, and the mature male from the latter group moved through the canopy of the tree it was feeding in to the side nearest the other male and looked across towards him. Both then resumed feeding, but broke off at intervals thereafter to look across at the other group.

The role of volley calls and explosive calls in intergroup spacing has already been discussed, in Chapter 5. That agonistic encounters are so rare despite the high population density seems to be due, firstly, to the spacing effects of these calls, and secondly to the relative tolerance of different groups, even at close quarters, provided each remains within its own range.

The C.aethiops populations in both Gartlan's and Struhsaker's main study areas were territorial, though this was not the case with a low density population at Chobi (Gartlan 1966). While a variety of calls may be given by C.aethiops groups during an encounter (Struhsaker 1967d) the species appears to lack any equivalent of the blue monkey's exchange of volley calls at other times. Both Gartlan (1966) and Struhsaker (1967e) describe 'jumping around' or 'branch shaking' displays, given by adult and sub-adult males, comparable to the 'bouncing' display of mature male blue monkeys. Likewise both authors describe a 'tail erect' posture assumed by males during intergroup encounters; this posture, however, was seen in the blue monkey only once, and then as a response by a female to the sudden appearance of the observer rather than in a social context. Gartlan (1966) recorded scent marking of territorial boundaries in the Lolui island vervets. Scent marking was not observed in the blue monkey. On one occasion, however, the mature male in group B was seen apparently sniffing a branch in the overlap zone between groups B and D's ranges; it walked very slowly and deliberately up the branch, pausing at frequent intervals and placing its nose against it.

The significance of territoriality is discussed in Chapter 9.

As already mentioned in Chapter 2, solitary males were sometimes encountered (see fig. 7.13). Such males were fully mature and apparently in the prime of life. Their relations with groups are uncertain. Presumably they must leave or become excluded from their group on attaining maturity, but it is not known how this comes about. Likewise it is not known whether they ever join a group again, or have any social contacts with group-living individuals.

Such evidence as is available suggests, though, that they normally have little if any contact with other monkeys. They tended to be found in the overlap zones between home ranges, and lower down in the canopy than group-living males. One of the mature males in group A was seen to perform the bouncing display on seeing a solitary male sitting in an isolated tree 100 yards out from the forest edge; the solitary male at once leapt down out of the tree and disappeared. Solitary males showed indications of nervousness such as urination or scratching on hearing explosive or volley calls from group-living males, and were never identified as making such noises themselves. It seems probable, therefore, that group-living males are intolerant of solitary males and that the latter tend to avoid them.

FIG.7.13 A solitary male.

SOCIAL STRUCTURE ... A DISCUSSION.

The patterns of behaviour in the blue monkey group have now been described. Our next task is to decide to what theoretical framework, if any, they can best be fitted.

Until recently it has been customary to consider primate societies in terms of dominance hierarchies. Dominance, as Gartlan (1968) has shown, has serious shortcomings as an explanatory concept, and much early writing on the topic was characterised by circular arguments and an unwillingness to modify the theoretical framework to take account of incompatible facts. Dominance was considered not as the outcome of complex social learning in the group as a whole but as the expression of some attribute of the individual dominant animal. In practice, though, hierarchies are generally maintained by the behaviour of the lower rather than the higher ranking animals, and the order of a hierarchy may vary greatly depending on the criteria used to define dominance, (see, for instance, Rowell 1966b). Attempts to define absolute rank by numerical weighting of the several criteria of 'dominance' serve merely to reify the purely abstract.

If these strictures are accepted, though, the

concept may nevertheless be retained, in some circumstances, as a purely descriptive device. Inasmuch as the outcomes of particular types of interaction are predictable they may conveniently be expressed in hierarchical form. A hierarchical model, however, will encompass only certain aspects of the behavioural relationships within the group; mother/infant behaviour, for example, would be outside its scope, and behaviour such as social grooming will not necessarily be correlated with any criteria of rank. Some primate populations lend themselves readily to such treatment; many baboon and macaque societies, for instance, can be described in this way. The blue monkey, on the other hand, exhibits a paucity of approach/retreat interactions, so the major features of its social behaviour cannot be described in hierarchical terms.

A few authors, having recognised the limitations of the concept of dominance, have sought recently to replace or supplement it by some alternative and more all-embracing descriptive device. For instance Bernstein (1966), Bernstein and Sharpe (1966) and Gartlan (1968) describe primate societies in terms of 'social roles', and it seems that the term 'role' may be on the verge of general acceptance in the

primatological literature. Before this comes about it seems important that the usage of the term should receive critical scrutiny. There is a particular need for caution since the word already has a variety of specialised meanings in sociological literature, many of which are clearly incompatible with any possible usage in the description of non-human primate societies, (cf. Reynolds, in press). Primate studies are a meeting point of many disciplines ... zoology, psychology, sociology, and anthropology ... and uncritical borrowing of terms from any one of these will serve only to increase the already not inconsiderable difficulties of communication.

Both Gartlan and to a lesser extent Bernstein and Sharpe use the term role with functional connotations. Thus for C.aethiops on Lolui Gartlan describes as roles a variety of behaviour patterns such as territorial display, social vigilance, and initiating group movements that he considers to be of adaptive significance in this particular habitat. Likewise Bernstein (1966) and Bernstein and Sharpe (1966) describe a role of 'control animal' in capuchin and rhesus monkey groups; this role is made up of behaviour patterns such as breaking up aggressive interactions between other group members, and moving

between a source of danger and the rest of the group.

While this approach is superficially attractive it raises certain difficulties. How is one to decide whether a particular pattern of behaviour is functional, whether to the individual or to the group as a whole? There are some senses in which all behaviour is functional, and hence a 'social role profile' for any animal would amount to a complete description of its behaviour. While such a description may be valuable it does not seem helpful to call it or its components roles. If, on the other hand, one restricts the use of the word to behaviour having some apparently clear cut adaptive value in a particular habitat, one's judgement of adaptiveness must necessarily rest on hypothesis, however plausible, rather than on established fact. For instance Gartlan considers 'jumping around' a form of territorial display in the vervet, as a role. This entails the assumption that because all vervet groups are territorial in the habitat under consideration, territoriality must be adaptive, and thus individuals that jump around are of functional value to the group. But is such behaviour general because it is of adaptive value to the individual, the group, or the population as a whole? Even if one decides

that it is adaptive at the group level, one still has no evidence on which to decide whether groups in which such behaviour was absent would be any less viable, other than the indirect evidence of there not being any such groups in the population. This sort of difficulty is of course common to much evolutionary theorising.

If the concept of role is superfluous as a purely descriptive term when applied to the whole range of behaviour of any individual, and its usage with functional connotations raises such difficulties, does it then have any value? Crook (1970a) has suggested that its use be restricted to denoting those sets of behaviour patterns that appear to be characteristic of the group, irrespective of the identity of the individual performing them. This meaning is implicit in Bernstein's usage of the term; for instance he records that the role of 'control animal' in a capuchin group was taken over by another individual when the original incumbent was removed. Thus the behaviour patterns making up the role are not the property of any individual animal; the role structure of the group remains relatively constant but the individuals filling the various roles may change. The network of behavioural

relations within the group is sufficiently complex to have a 'buffering' effect; if one animal is removed the behaviour of those remaining is modified in such a way as to re-establish equilibrium, (see also Reynolds, in press).

If one does use role in this restricted sense, and clearly some word is needed to describe such clusters of behaviour patterns, then only certain aspects of behaviour will fall within its scope. Hence behavioural relations as a whole cannot be described purely in terms of roles. Our knowledge of the blue monkey is anyway insufficient to permit the identification of such roles.

An alternative approach is to construct 'behaviour profiles' for individual animals, or histograms showing the contributions of individuals to particular activities. Such profiles would be comparable to Gartlan's 'social role profiles', but would include all activities rather than just those considered as roles. They would be purely descriptive. Consider, for instance, the data on grooming in fig. 6.9. The row totals could be plotted as a histogram showing the contribution of each class as a whole to the observed total of grooming. This procedure could be followed for other

activities such as play or aggression. Alternatively the same information could be grouped by classes, separate histograms for each class showing the frequency with which it indulged in the various activities.

While these procedures would show the contribution of each class to the behaviour of the group, it would not be immediately apparent whether differences in these contributions were the result of contrasts in behaviour or merely of differences in the numbers of monkeys in each class. If females as a whole groom more than males, for example, is this because the individual animals behave differently, or merely because there are more females than males in the population? While this question could be answered by incorporating expected values in the histograms, the resultant diagrams would be too cumbersome to be readily interpreted (cf. Chalmers 1968b).

This difficulty can be overcome by plotting histograms for hypothetical average individuals of each class. Consider the row totals in fig. 6.9 once again. Mature males were seen to groom other monkeys 11 times. Since the four groups from which the data were drawn contained 5 mature males, an

average mature male would groom 11/5 times, i.e. 2.2. Likewise the 188 grooming records for females were obtained from a theoretical 21.5 monkeys; hence the average female would groom 8.74 times. The advantage of such a system is that since one is dealing with individuals rather than classes the expected values are the same for each individual, and any departures from expectancy are readily apparent. This approach can be criticised in that there may be substantial variations in behaviour within each class, and hence that the hypothetical average monkeys are not truly representative. While there may indeed be considerable contrasts in behaviour between members of the same class, the difficulty of recognising individuals makes the quantification of such differences impossible. Since one has anyway to make one's analysis in terms of classes rather than individuals, it makes little odds whether one considers classes as a whole or average individuals of each class; both approaches have the same shortcomings.

Fig. 7.14 gives histograms, constructed on this basis, for all the activities described in preceding sections. The number of times that the average

individual of each class played both an active and a passive part in the various types of interaction is shown; for instance the histogram for grooming shows the number of times that each class both groomed and was groomed, and that for mounting the number of times each both mounted and was mounted. In the histogram for sitting associations the lower part of each column represents associations in the absence of any overt interaction, and the upper part associations before or after interactions such as grooming. It must be remembered that values for young males and for females are likely to be underestimates, due to the large number of interactions in which adults were unsexed.

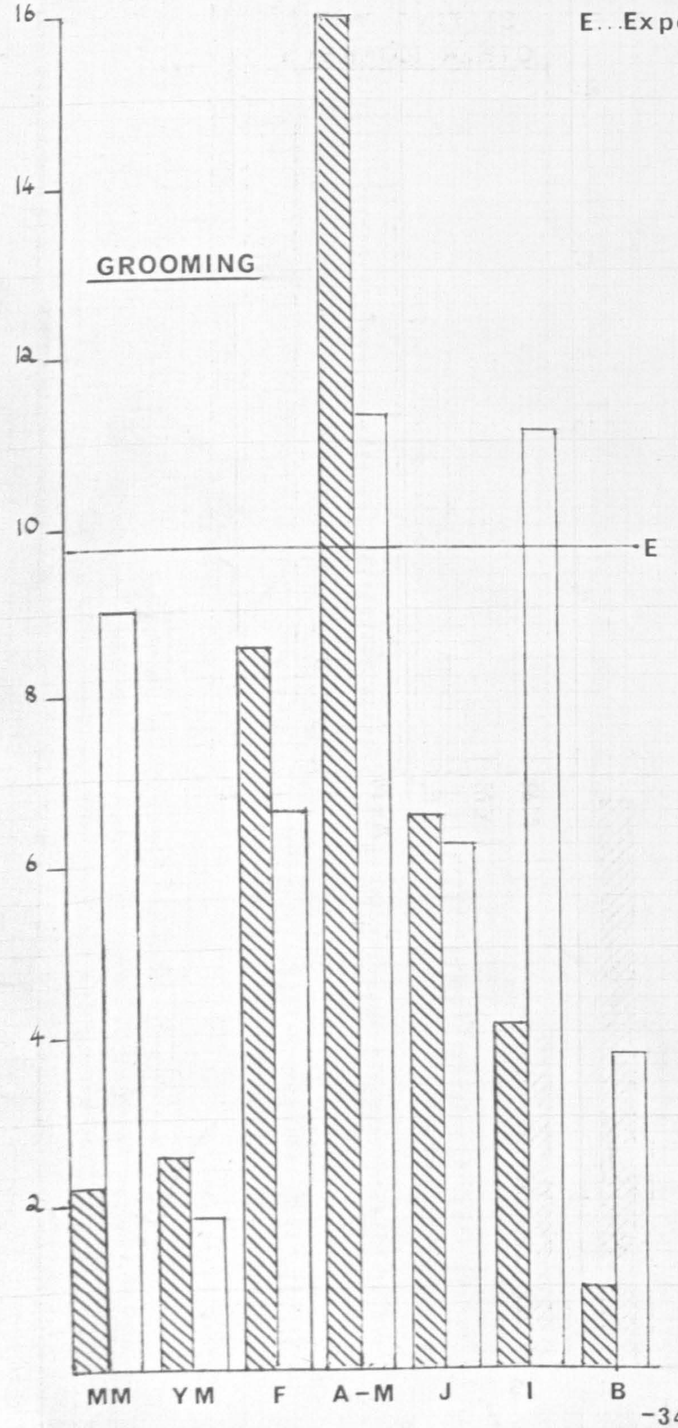
Salient features in the distribution of each activity stand out clearly. For example the grooming histogram shows that adults other than mature males both groom and are groomed more than expected, infants are groomed more than expected but groom less, and other classes both groom and are groomed less. Mature males, infants, and babies are groomed more than they groom, while adults other than mature males groom more than they are groomed. Similarly the histogram for play shows that infants play more than expected, juveniles about as much as expected, and other classes less.

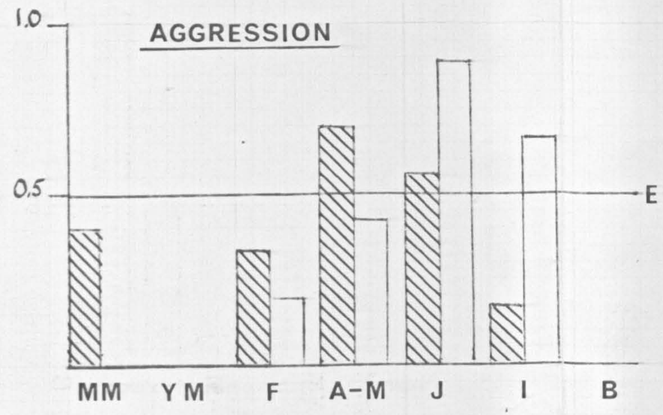
FIG. 7.14 CONTRIBUTIONS OF AVERAGE INDIVIDUALS OF EACH CLASS TO VARIOUS ACTIVITIES.

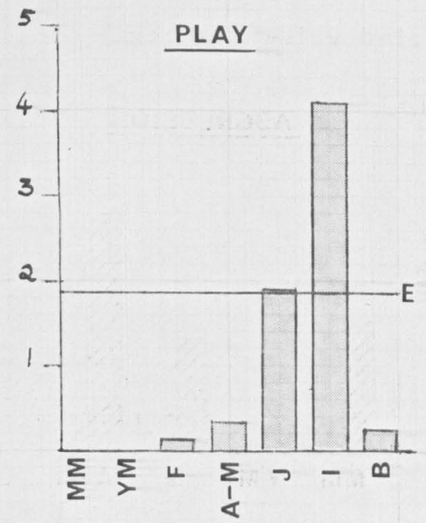
Active partner in interaction

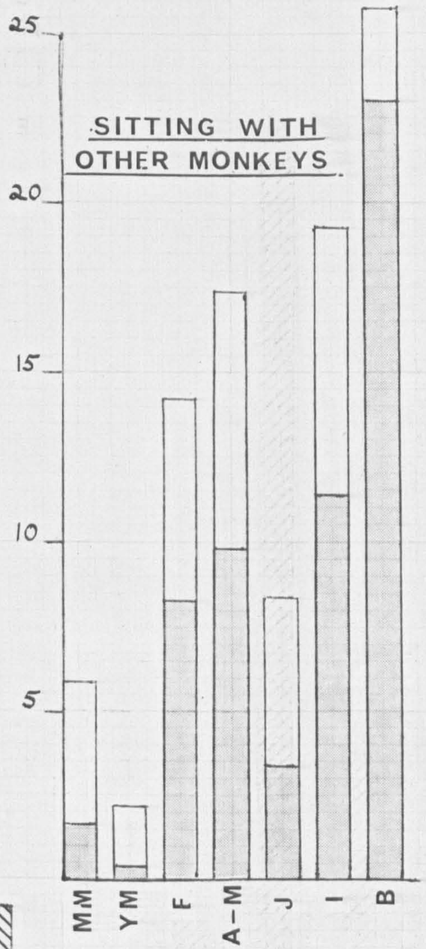
Passive partner

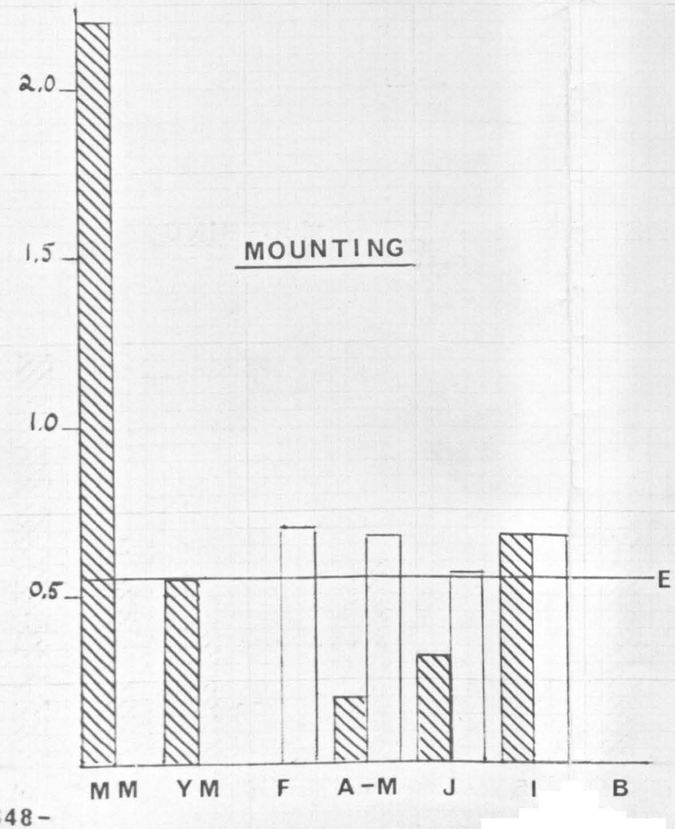
E...Expected value (see text)











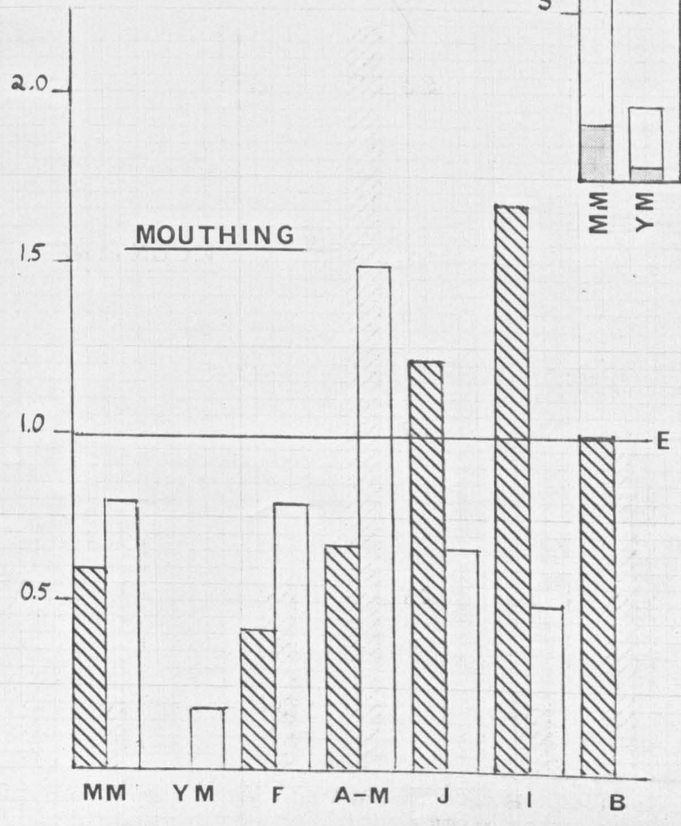
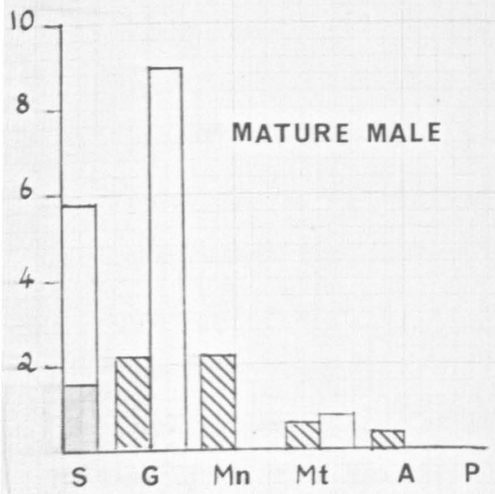
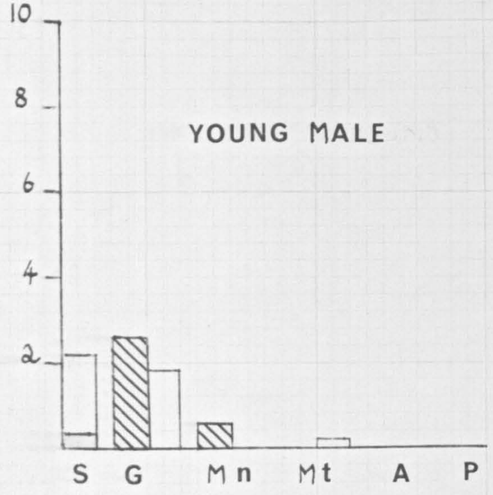
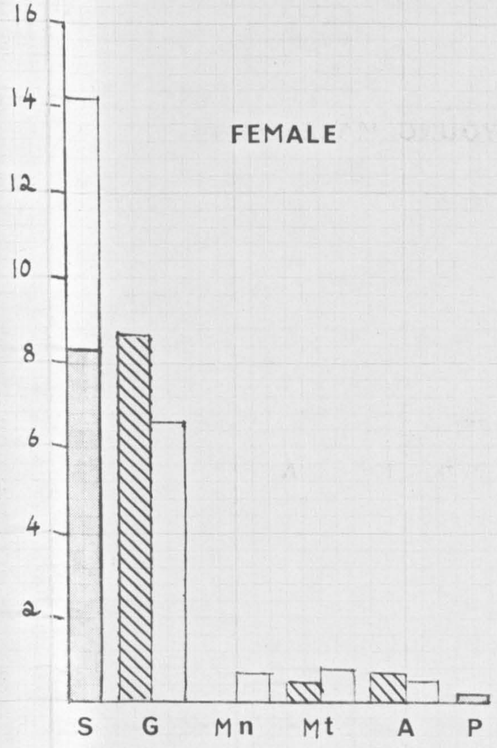
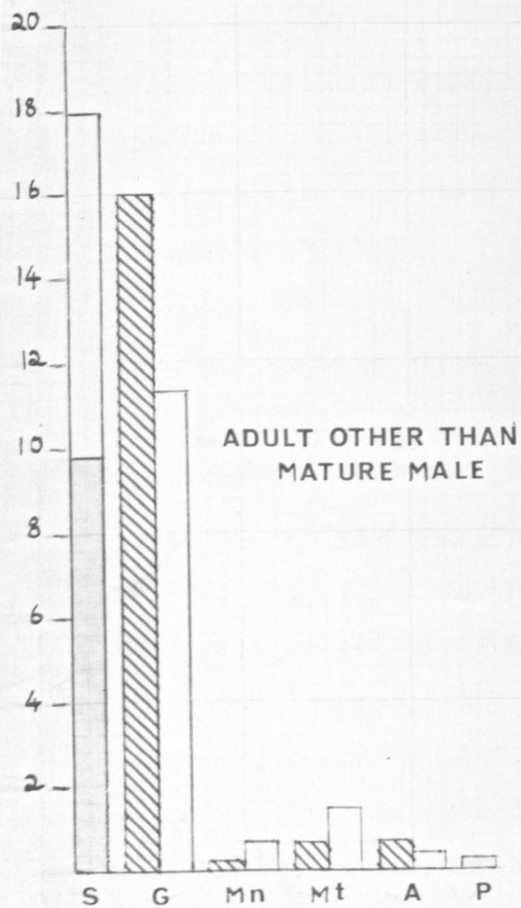


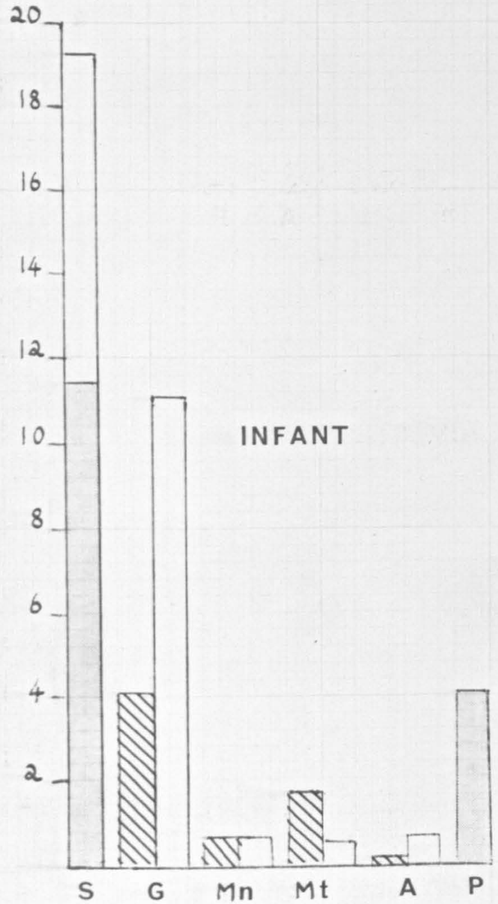
FIG. 7.15 'BEHAVIOUR PROFILES' FOR AVERAGE INDIVIDUALS OF EACH CLASS

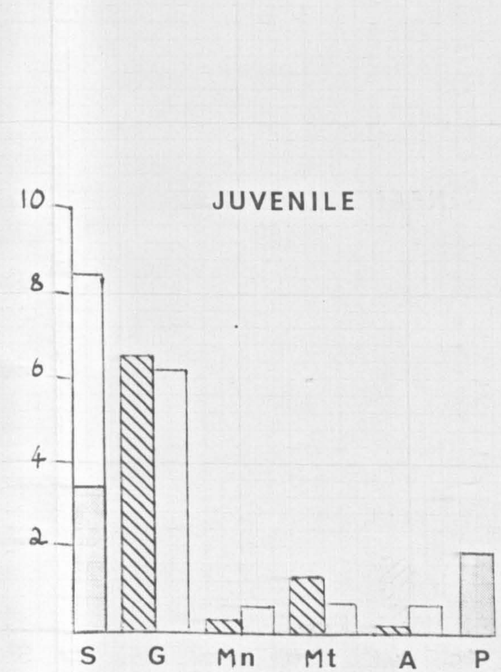


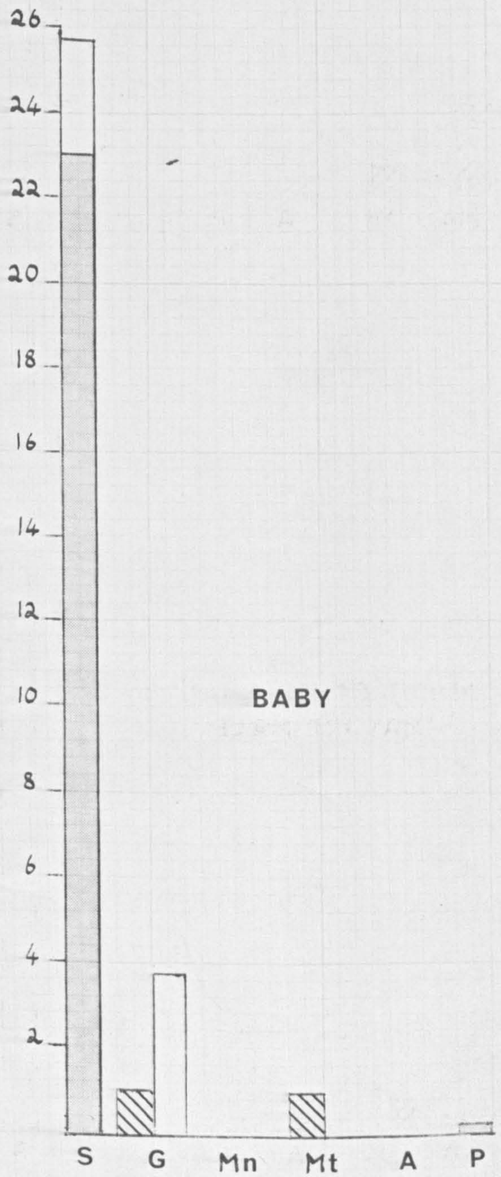












KEY: S...Sitting G...Grooming Mn...Mounting. Mt... Mouthing. A...Aggression. P... Play.

Fig. 7.15 presents the same data grouped by classes rather than by activities, giving 'behaviour profiles' for the average individual of each class. Once again the number of times such individuals both performed and received behaviour such as grooming or mounting is shown. There are clear differences between classes, both in the overall numbers of interactions in which each is involved and in the relative frequencies of the different types of behaviour.

Such profiles provide a useful summary of the behaviour of each class, and would be of value in comparing the social structure of different species. Their major shortcoming is that they tell one little about the relations <u>between</u> individuals or classes. Fig. 7.15 shows, for example, that adults other than mature males groom more than other classes, but it does not tell us which classes they groom. Details of the relationships between classes have emerged during the analysis of the various behaviour patterns, but there is a need for some means of summarising these findings.

One possible course is to describe social structure in terms of affinities between the age/sex classes, (cf. Kummer 1968). If two animals are involved in some friendly interaction such as social

grooming, one could take this to be indicative of a positive affinity between them. Conversely interactions having an approach/retreat pattern would be indicative of negative affinities. The spatial relations between individuals could likewise be taken as measures of affinity; thus animals that sit together frequently would have a stronger affinity than ones that sit together only rarely. Kummer found that in the hamadryas there was a strong correlation between spatial and interactional measures of affinity between some classes, suggesting that both may be measuring the same thing, but that this was not true of other classes. He suggests that this may be because the relations between two classes are affected by the presence of a third class. Such complications are perhaps less likely to arise in the blue monkey, since individuals are typically more widely scattered than is the case in the hamadryas one male unit.

An inherent danger of such a course is that one runs the risk of blurring the distinction between explanatory and purely descriptive concepts. If one has <u>categorised</u> certain patterns of behaviour such as grooming or sitting together as friendly, one cannot then <u>explain</u> the observed frequencies of

interaction by postulating 'bonds' or 'affinities' between the animals concerned. The motivations underlying affinities between the classes are clearly various. A male copulating with a female and a female grooming an infant, for instance, would both be taken as indications of positive affinity. Moreover the same patterns of behaviour may at times be associated with different underlying motivations. The interpretation of grooming interactions, for example, is, as we have already seen, particularly complex.

Bearing in mind these limitations on the use of the term, what, in the purely descriptive sense, are the major affinities in the blue monkey group? It will be recalled that the outstanding feature of social grooming, by far the commonest type of interaction, was a superfluity of female/female and female/infant interactions. As regards sitting associations, females and babies sat together more than would be expected on a random basis, and the same was true, to a lesser extent, of females and infants. On the other hand juveniles and mature males played little part in grooming and were seldom seen in association with other monkeys. Thus the strongest affinities in the group would appear to

be these between females and babies, infants, and other females. Mature males and juveniles have comparatively weak affinities with other animals, and the same is probably true of young males.

It is tempting to use this outline of the blue monkey's social structure as a basis for comparison with other species. The temptation should be resisted. While providing a convenient summary of certain aspects of behaviour, it is far removed from actual hard data. The same would be true of similar descriptions of other species. The use of such summaries as a basis for comparison might equate totally different relationships. In one species, for instance, most friendly interactions between males and females might be grooming interactions, while in another they might be copulations, yet both species might be said to have a strong affinity between the two sexes. It cannot be stressed too strongly that interspecific comparisons should be on the basis of actual data rather than of abstractions from those data, irrespective of the concepts used. Primate societies are highly complex; concepts such as hierarchy, role, and affinity are descriptively convenient but inevitably involve oversimplification, and may, if used uncritically, be positively misleading.

Chapter 8

RELATIONS WITH OTHER SPECIES

RELATIONS WITH OTHER NON-HUMAN PRIMATES.

Introduction.

Four other diurnal primates besides the blue monkey are found in Budongo, the redtail, Cercopithecus ascanius, the black and white colobus, Colobus guereza, the olive baboon, Papio anubis, and the chimpanzee, Pan troglodytes, (see figs. 8.1 - 8.4). All are common, and were often encountered while I was searching for or watching blue monkeys; hence I was able to collect much incidental information on them and their relationships with the primary subject of the study.

Since most of the data for species other than the blue monkey presented in this chapter were collected during such incidental encounters, they do not give an entirely unbiased picture of the behaviour and distribution of the various species. My movements through the forest were not random, but were influenced by the likelihood of encountering blue monkeys in particular localities. The chances of species other than blue monkeys being seen were therefore to some extent related to their degree of association with blue monkeys.

FIG.8.1 A redtail monkey, Cercopithecus ascanius.

FIG.8.2 A party of black and white colobus, Caguereza.

FIG.8.3 A baboon, Papio anubis.

FIG.8.4 A chimpanzee.

In an attempt to overcome this difficulty a series of strip censuses was carried out. A 1000 yard transect was walked at a steady pace, between 0730 and 0900 hrs, and the location, activity, and level in the canopy of all monkeys seen within 50 yards on either side of the track were recorded. Two tracks, one running through the main study area and one through an area ¼ mile to the west of it, were used for censuses. Whenever possible each area was covered twice a month from July 1966 until the end of the study, and in all 24 such censuses were made. It was hoped that these would provide unbiased information on the relative abundance of the various species in the area as a whole and in the different forest types, and show whether they had any tendency to associate or avoid one another. Unfortunately the number of sightings proved insufficient to achieve these aims; only 58 parties of monkeys were seen in the 24 censuses and on four none were seen at all. The results are of value, therefore, only as a pointer to the degree of bias in the much larger sample of incidental information. It proved impracticable to devote more time to censuses in the present study (see Chapter 1), but in a project concerned exclusively with interspecific

relations a greater concentration on censuses would undoubtedly be worthwhile.

Occurrence of mixed species parties.

Many previous workers have noted the occurrence of mixed species parties in forest monkeys. Haddow (1952), for example, gives many instances of redtails associating with one or more other species in Uganda, Chalmers (1968a) records mixed parties of Cercocebus albigena, Cercopithecus mitis, and Colobus badius in the Kibale forest, Booth (1957) observed mixed parties of Colobus and Procolobus spp in West Africa, and both Struhsaker (1969) and Gartlan (pers.comm.) noted mixed parties of Cercopithecus spp in Cameroon. Detailed quantitative studies are at present limited to those of Bernstein (1967) on Macaca, Presbytis, and Hylobates spp in Malaya, and Gautier and Gautier-Hion (1969) on Miopithecus, Cercopithecus, Cercocebus, and Colobus spp in Gabon. The latter study in particular provides many interesting contrasts with the present findings.

Mixed species parties were commonly encountered in Budongo. Fig. 8.5 gives the number of sightings of single and mixed species parties in the 24 censuses.

The criterion of a mixed party was that the different species should be less than 50 yards from one another, though in most cases the association was much closer and the various species completely intermingled. Fig. 8.6 gives details of all sightings of each species between July 1966 and March 1967. It must be remembered that this gives a reliable picture of the tendency to form mixed parties only for the blue monkey, and not for the remaining species. For these the tendency to associate with blue monkeys will be exaggerated and to associate with one another or be found in single species parties diminished. For example of 121 sightings of redtails 49 (40.5%) were of mixed parties, 44 of them with blue monkeys, but this cannot be taken to indicate that the redtail spends 40% of its time in mixed parties. The figure of 20% for mixed parties recorded in the censuses, though admittedly based on a much smaller sample, is probably a closer approximation to the truth.

For the blue monkey, though, the data are not subject to any such bias and the larger sample can be taken as representative. Of 354 encounters with blue monkeys, 292 (82.5%) were of single species parties, and 62 (17.5%) of mixed parties. Of the 62

FIG.8.5 Occurrence of single and mixed species parties in censuses.

SPECIES	SINGLE	MIXED	TOTAL
Blue monkey	22	2	24
Redtail	11	4	15
Colobus	10	2	12
Baboon	4	1	5
Chimpanzee	2	-	2
TOTAL	51	7	58

FIG.8.6 Occurrence of single and mixed species parties, all sightings July 1966 - March 1967.

SPECIES	Single species parties.	Mixed parties with: Blues	Redtails	Colobus	Baboons	Chimps	TOTAL MIXED	GRAND TOTAL
Blue monkey	292	-	44	16	1	6	62*	354
Redtail	72	44	-	5	1	4	49*	121
Colobus	67	16	5	-	-	-	20*	87
Baboon	15	1	1	-	-	-	2	17
Chimpanzee	33	6	4	-	-	-	6*	39
TOTAL	479	67	54	21	2	10	139*	618

* Since some mixed parties contained three species, these totals may be less than the sum of the number of mixed parties with individual species. Five such trispecific parties were recorded: 4 blues/redtails/chimps and one blues/colobus/redtails.

mixed parties 57 were bispecific and 5 trispecific. Mixed parties appeared to be slightly more frequent during the rainy season, 43 (19.5%) of 220 sightings, when fruit was abundant, than during the dry season when leaves and young shoots constituted the greater part of the diet, 19 (14.2%) of 134 sightings, but this difference is not statistically significant. (X^2 = 1,683, with one degree of freedom).

In contrast Gautier and Gautier-Hion found that the frequency of mixed parties in their study area in Gabon was much higher, associations of two or more species being the rule rather than the exception. (Neither these authors nor Bernstein give a precise definition of what they mean by 'mixed parties' or 'multiple sightings', but contrasts between the results in the various study areas are considered too great to have arisen purely through differences in recording methods). For instance in primary forest at Belinga 28 (85%) of 33 encounters with Cercopithecus nictitans, 23 (90%) of 26 encounters with C.cephus, 18 (80%) of 23 encounters with C.mona, and 6 (75%) of 8 encounters with Cercocebus albigena were of mixed parties. With the exception of Cercopithecus neglectus, which was invariably recorded alone, in no area was the frequency of mixed parties for any species less than

46%. Bernstein (1967) found that the chances of multiple sightings in his study area ranged from 23% for Macaca nemestrina to 53% for Hylobates lar, again higher than in the present case.

Fig. 8.6 suggests that the various species differ in the relative likelihood of their being found in association with blue monkeys. Thus 36% of all sightings of redtails were of mixed parties with blue monkeys, while 18% of colobus sightings, 15% of chimp sightings, and only 1 (6%) of the 17 sightings of baboons were of such parties. Fig. 8.7 gives the observed numbers of such parties, together with the expected numbers were there no differences in the tendency of each species to associate with blue monkeys. X^2 is calculated as 15.42, for which with 3 degrees of freedom $p =< 0.01$. Hence there is a definite association between species and the formation of mixed parties with blue monkeys. Similarly comparison of individual pairs of species shows that redtails are more likely to be found in the company of blue monkeys than are colobus ($X^2 = 7.97$, $p =< 0.01$), chimps ($X^2 = 6.06$, $p =< 0.05$), or baboons ($X^2 = 6.20$, $p =< 0.05$. One degree of freedom in each case.). No such difference can be shown between colobus and chimps ($X^2 = 0.165$), and

FIG.8.7 Relative tendencies of other species to associate with blue monkeys.
(Expected values were all species equally likely so to associate in brackets).

SPECIES	WITH BLUES	WITHOUT BLUES	TOTAL
Redtail	44 (30.7)	77 (90.3)	121
Colobus	16 (22.1)	71 (64.9)	87
Chimpanzee	6 (9.9)	33 (29.1)	39
Baboon	1 (4.3)	16 (12.7)	17
TOTAL	67	197	264

the data are insufficient to permit similar comparison between colobus and baboons or chimps and baboons. These findings are in accordance with qualitative behavioural observations (see below).

A comparable state of affairs was found by Gautier and Gautier-Hion in Gabon; some associations were much more frequent than others. C.nictitans, for instance, was often found with C.cephus or C.mona, while the two latter species were seldom found together except when associated with C.nictitans in trispecific parties. Similarly Bernstein found that the probability of pairs of species being found together varied from 0.04 for H.lar and P.obscurus to 0.45 for H.lar and P.melalophus.

Duration and behaviour of mixed species parties.

The mixed parties encountered in Budongo appeared to be chance aggregations of brief duration rather than long term, organised associations. In no case were two species seen to associate for more than a few hours, and while mixed parties might be seen on several successive days at favourable feeding sites the various species usually arrived and left separately. Most mixed bands of blue monkeys and redtails and all the mixed parties of

blue monkeys and chimps were observed on local concentrations of food such as fruiting Pseudospondias or Ficus spp. Colobus, on the other hand, overlapped less with blue monkeys in their diet, and the two species were usually seen together when blue monkeys were travelling through trees in which the more sedentary colobus were feeding or resting.

This pattern is a marked contrast to that noted by Gautier and Gautier-Hion in Gabon, where in areas free from human disturbance the same mixed parties might be found in the same areas not only from day to day but also from year to year. These authors also noted that mixed bands were more frequent in the evening than in the morning, the different species coming together to sleep. No comparable change in the frequency of mixed parties was seen in Budongo.

The mixed groups observed by Bernstein in Malaya appeared to be intermediate in their stability. Most were in the nature of temporary aggregations at feeding sites, though in some cases troops of different taxa might coordinate both travel direction and speed despite ordinarily disparate rates of progression. One pair of gibbons, though, was regularly associated with a troop of P.melalophus,

and the male gibbon appeared to be established in the social organisation of the melalophus troop. Comparable cases have been noted in other studies; Jay (1965) describes a female rhesus monkey living with a group of langurs, and T.E. Rowell (pers.comm.) records a male vervet monkey as living with a troop of baboons and even mating with the females.

Behavioural interactions between blue monkeys and redtails or colobus were generally limited to taking note of the other species' alarm calls (see Chapter 5). Individuals would pass within 3 ft. of one another without any obvious interaction. On two occasions blue monkeys chased and threatened redtails when the two species were feeding together in a fruiting fig tree, and on one of these the redtails were driven out of the fig tree altogether, but such incidents were exceptional. As a rule the two species would feed together quite peacefully and appeared to ignore one another. An adult redtail was seen successfully to solicit grooming from an adult blue monkey at the second attempt; the postures used to solicit grooming are basically similar in the two species. Interactions between them must sometimes go further than this, as the hybrid in group B shows, but interbreeding must be

very rare since the two species are found together over much of their range in Uganda and yet remain quite distinct. On the other hand Clutton-Brock (pers.comm.) reports that blue monkeys and redtails in the Gombe Stream reserve in Tanzania interbreed widely, and are presumably fertile (as in the present case) since all forms of intermediate are found.

Only one clear cut interaction between blue monkeys and colobus was seen; a mature male blue monkey moved out of the way of an adult colobus which rushed along a branch towards it after seeing me. In the Kibale forest in western Uganda mixed parties of blue monkeys and red colobus, Colobus badius, were observed, and a blue monkey was seen being groomed by a red colobus.

The relation between blue monkeys and chimpanzees is markedly different to that between blues and red-tails or colobus. The two species were never seen in close proximity, and chimpanzees appeared to be avoided by monkeys. On four occasions parties of blue monkeys were seen to move out of trees in which they had been feeding when chimps approached. In the few instances in which blue monkeys were seen to feed in the same trees as chimps, they always kept at least 10 yards from them, and moved across into

the next tree if the chimps approached any closer or made any sudden movements. Redtails behaved in a similar way. A chimp was once seen to make a sudden rush towards a juvenile and infant blue monkey and infant redtail as if trying to catch them. It is known that chimpanzees have carnivorous propensities; Suzuki (quoted in Sugiyama 1968b) saw chimps eating a blue monkey and a black and white colobus in Budongo, and Van Lawick-Goodall (1968) has observed them killing and eating young baboons and red colobus. Baboons also might kill monkeys if given the chance; only one blue monkey, a mature male, was ever seen feeding in the same tree as baboons, and it is known that the latter kill and eat small mammals (Dart 1963, Washburn and DeVore 1963, Rowell 1966a).

Ecological relations between species.

It is generally assumed that closely related species can coexist in the same region only if they are exploiting different aspects of the environment, and hence maintaining competition at a minimum. For example Crook and Aldrich-Blake (1968) were able to show that sympatric populations of Theropithecus gelada and Papio anubis in Ethiopia overlapped but little in their use of the habitat. The presence of

five primate species in the same forest, and in particular of two Cercopithecus spp. with a tendency to form mixed parties, thus raises the question of whether such ecological separation can be demonstrated.

Separation could be achieved in several ways. The various species might differ in their relative frequency in different parts of the forst; some, for instance, might prefer colonising forest and others mature forest or swamp forest. If several species were found together in the same area, there might be a stratification of species in the canopy. Even if no such spatial separation could be shown, actual competition for food might be minimised by contrasts in diet. In the present case it seems that all three of these factors operate to some extent.

Fig. 8.8, based on all encounters with primates between 25/6/66 and the end of the study, gives the number of sightings of individuals of each species more than 100 yards inside the forest, within the forest but less than 100 yards from the edge, and outside the forest. It can be seen that redtails are found within 100 yards of the forest edge more often than are blue monkeys or colobus, approximately 45% of all records as against 35% and 37% respectively. This difference is statistically significant; for

FIG.8.8 Relative abundance of different species at various distances from the forest edge.

SPECIES	>100 yards	<100 yards	Outside forest	TOTAL
Blue monkey	925 (65.2%)	492 (34.7%)	2 (-)	1419
Redtail	248 (55.0%)	202 (44.8%)	1 (0.2%)	451
Colobus	230 (62.7%)	137 (37.3%)	-	367
Baboon	31 (20.9%)	86 (58.1%)	31 (20.9%)	148
Chimpanzee	52 (15.7%)	3 (0.9%)	276 (83.4%)	331

blue monkeys and redtails X^2 = 15.3, for which p =< 0.001, and for colobus and redtails X^2 = 4.89, for which p =< 0.05 (one degree of freedom in each case). On the other hand no such difference can be shown for blue monkeys and colobus (X^2 = 0.8). This finding is in accordance with Haddow's (1952) observation that redtails in other parts of Uganda preferred colonising forest and secondary growth on the edges of roads and clearings to mature high forest.

Blue monkeys, redtails, and colobus are clearly confined to the forest, a negligible proportion of sightings being outside its limits. For baboons and chimpanzees the picture is very different. Baboons are based on the forest edge and forage a short way into the forest and out into the savanna. It must be remembered that the figures in fig. 8.8 are purely relative; the absolute amount of time spent by baboons outside the forest is probably much greater than the 21% indicated. Of the 131 baboon sightings within the forest 86 (73.5%) were less than 100 yards from the edge, a marked contrast to the three previous species. A possibly comparable state of affairs was found by Lamprey (1963) in the Tarangire reserve in Tanzania; certain ungulate species were

seen more often on the boundary between distinct ecological zones than within any one zone. Presumably species with sufficient adaptability are thus enabled to take advantage of the differing resources offered by each zone.

For chimpanzees the figures are somewhat misleading. Taken at face value they would seem to indicate that chimps are savanna rather than forest animals. The great number of records of chimps outside the forest is due, however, to the sighting of several large parties of 20 to 40 individuals crossing from the study area to another patch of forest, separated by the road and 300 to 400 yards of grass, to the west. These parties were very noisy when approaching the forest edge and nearly always crossed the road at the same spot, so they attracted attention from a distance and could readily be counted. On the other hand chimps within the forest were less obtrusive and more difficult to see; records for chimps inside the forest are therefore disproportionately few. Of those chimps that were seen inside the forest the great majority were more than 100 yards from the edge. It seems that as Reynolds and Reynolds (1965) suggest chimps range over a wide area of forest, their distribution being

closely related to short term concentrations of food such as fruiting Pseudospondias, Maesopsis, or Ficus spp. When such trees were fruiting in the study area chimps could be seen on several successive days. At other times none might be seen for as long as a month, implying that they ranged over a much greater area of forest than the remaining species.

In Chapter 3 data were presented showing that blue monkeys were not seen equally often in all layers of the canopy, but tended to be found in the middle rather than the lower or upper layers. Fig. 8.9 gives comparable data for the same period for the other four species as well. It can be seen that while no species confines itself exclusively to any layer there is some stratification of species in the canopy, colobus tending to occupy higher and redtails lower levels than blue monkeys, with baboons and chimps being largely terrestrial. (The possibility of differences in the relative visibility of species in the various canopy layers is considered too remote to invalidate this conclusion). In fig. 8.10 are shown total sightings of each of the three arboreal species in the different layers for the wet and dry seasons separately and for both seasons combined, together with expected values were there no association between species and canopy layer. Observed

FIG.8.9 Activity and zonation of species, 25/6/66 - 17/3/67.

SPECIES	Ground				Lower canopy				Middle canopy				Upper canopy				TOTAL
	F	S	M	T	F	S	M	T	F	S	M	T	F	S	M	T	
Blue monkey	-	1	3	4	209	190	61	460	544	630	305	1479	370	306	77	753	2696
Redtail	-	1	-	1	33	36	75	144	72	59	125	256	29	5	4	38	439
Colobus	-	-	-	-	13	9	17	39	38	82	42	162	17	141	9	167	368
Baboon	-	38	47	109*	4	17	6	27	2	7	-	9	-	3	-	3	148
Chimpanzee	-	-	276	276	3	1	2	6	31	2	9	42	6	1	-	7	331

* Includes 24 activity unclassified.

Activities: F... feeding, S... sitting, M... moving. T... total for individual layer.

FIG.8.10 Stratification of arboreal species, all activities combined.

(Observed values and percentages above, expected values below)

WET SEASON.

SPECIES	Lower canopy*	Middle canopy	Upper canopy	TOTAL
Blue monkey	184 (13.3%) 211	798 (57.9%) 802	397 (28.7%) 365	1379
Redtail	90 (27.9%) 50	215 (66.6%) 188	18 (5.5%) 85	323
Colobus	8 (5.8%) 21	57 (41.6%) 80	72 (52.6%) 36	137

DRY SEASON.

Blue monkey	280 (21.3%) 290	681 (51.7%) 655	356 (27.0%) 373	1317
Redtail	55 (47.4%) 25	41 (35.3%) 58	20 (17.2%) 33	116
Colobus	31 (13.4%) 51	105 (45.4%) 115	95 (41.1%) 65	231

BOTH SEASONS COMBINED.

Blue monkey	464 (17.2%) 499	1479 (54.9%) 1460	753 (27.9%) 737	2696
Redtail	145 (33.0%) 81	256 (58.3%) 238	38 (8.7%) 120	439
Colobus	39 (10.6%) 68	162 (44.0%) 199	167 (45.4%) 101	368

* Includes records for ground(see fig.8.9).

FIG.8.11 Stratification of feeding activity in arboreal species.
(Observed values and percentages above, expected values below)

SPECIES	Lower canopy	Middle canopy	Upper canopy	TOTAL
Blue monkey	209 (18.6%) 216	544 (48.4%) 554	370 (32.9%) 353	1123
Redtail	33 (24.6%) 26	72 (53.7%) 66	29 (21.6%) 29	134
Colobus	13 (19.1%) 13	38 (55.8%) 34	17 (25.0%) 21	68

values depart significantly from expectation in each case; for the wet season X^2 = 145.6, for the dry season 70.8, and for the two seasons combined 173.4, p =< 0.001 with 4 degrees of freedom in each case. Separation of the three species is greater, however, in the wet than in the dry season; for the wet season X^2/n = 0.0792 and for the dry season 0.0425.

It will be recalled that blue monkeys were found at lower levels in the canopy in the dry season than during the rains. The same is true of both redtails and colobus; comparison of zonation within each species between seasons yields for redtails X^2 = 38.5, for which p =< 0.001, and for colobus X2 = 6.82, for which p =< 0.05, with two degrees of freedom in each case.

Each species, then, has a preference for a particular level in the canopy. As regards ecological separation, though, the critical point is not the overall time spent in each layer ... there is no competition for space as such ... but the amount of feeding in each layer. Fig. 8.11 gives the observed totals and percentages of feeding records for each species at the three canopy levels, together with expected values were there no association between species and canopy layer.

Information for wet and dry seasons is combined, since there are insufficient data in certain categories to allow them to be treated separately. X^2 is calculated as 8.73, which with 4 degrees of freedom is not significant. However if pairs of species are considered separately a different picture emerges. There is a significant separation between blue monkeys and redtails (X^2 = 7.72, $p =< 0.05$, X^2/n = 0.006), but no such separation between blue monkeys and colobus (X^2 = 1.99, X^2/n = 0.001), or between redtails and colobus (X^2 = 0.87, X^2/n = 0.004. Two degrees of freedom in each case). Thus the two Cercopithecus spp, both of which eat a variety of fruits, flowers, and young shoots, overlap less with one another than they do with the more distantly related and exclusively leaf eating colobus. Potential competition for food is greater (see bdow), but is partially reduced by differences in feeding level. Colobus, on the other hand, can feed at the same level as the Cercopithecus spp with only limited competition.

It has frequently been stated in the past that forest primates occupy different levels in the canopy (e.g: Napier 1962, Napier and Napier 1967),

but apart from Booth's (1957) observations on the stratification of Colobus and Procolobus spp in West Africa there is little evidence for this assertion. While it can be upheld to some extent in the present case, Gautier and Gautier-Hion (1969) found that in primary forest in Gabon there was no such stratification between Cercopithecus nictitans, C.cephus, and C.mona. The more exclusively leaf eating Cercocebus spp and Colobus polykomos were, however, found at higher levels than these three species. In Malaya Bernstein (1967) recorded 20% of M.nemestrina sightings on the ground and another 19% in the lower canopy, while approximately 90% of all sightings of M.irus, P.obscurus, and H.lar and 82% of P.melalophus sightings were in the middle and upper layers. Vertical separation between the four latter species was thus not marked.

The collection of detailed comparative information on the diet of the various species was not practicable. I gained the impression, however, that the diet of the redtail was basically similar to that of the blue monkey ... at least half of the important items in the latter's diet were eaten . also by redtails ... but that redtails spent more time eating creeper berries and young shoots low down

in the canopy than did blue monkeys.. In contrast colobus were almost exclusively leaf eaters, and while they seemed to prefer young shoots to old leaves the latter appeared to account for a large proportion of their diet. Competition between colobus and the two Cercopithecus spp. would therefore be limited.

Of the 25 species of tree whose fruits were eaten frequently by blue monkeys 12 were recorded by Reynolds and Reynolds (1965) as being eaten by chimpanzees in Budongo, and the most important chimp foods, the fruits of Pseudospondias, Maesopsis, and Ficus spp, were all major items in the blue monkey's diet as well. There is no doubt that chimps must greatly reduce the available food for blue monkeys and redtails. When the fruit on a fig tree was ripening monkeys would visit it and feed selectively on the riper fruits, but once the main crop became ripe chimps would move in and the monkeys be driven out. Chimps might remain in fruiting trees for several hours a day, so denying their use to the monkeys, and a heavy crop of fruit might be completely stripped in less than a week. The effective fruiting period of individual trees as far as the monkeys were concerned was therefore greatly reduced.

Little information is available on the diet of

baboons in Budongo, but they were seldom seen to feed on the same plants as blue monkeys and appeared to obtain much of their food at ground level. Uprooted Marantochloa plants with the soft base of the stem eaten away were often found after the passage of a troop of baboons.

Apparent overlaps in diet may be minimised by morphological contrasts between species. For instance both blue monkeys and baboons eat the pods of the ironwood, Cynometra alexandri, but blue monkeys are only able to do so when they are young and soft. At a later stage they harden and become too tough for blue monkeys, but not for baboons. Conversely adult baboons are too heavy to climb among thin twigs, and so are less able to exploit all the potential food in trees such as Maesopsis, in which the fruits are borne at the extremities of the canopy, than are lighter monkeys such as blues or redtails.

In summary then, baboons are based on the forest edge and forage out into the savanna and a short way into the forest, redtails are found in young colonising forest and in secondary growth along the edge of tracks and clearings, and the remaining species are found deeper into the forest. There is some stratification of species in the canopy, colobus

occupying the upper, blue monkeys the middle, and redtails the lower layers. Baboons and chimps are based on the ground, but may ascend into the canopy to feed. There are varying degrees of overlap in diet, blues and redtails overlapping substantially with one another and with chimps, but less with colobus and baboons.

Discussion.

The presence of many primate species in the same region raises several questions regarding the evolutionary origins and ecological and behavioural maintenance of such diversity. As a general rule diversity of species is far greater in forest than in open country; some forests have as many as ten species of monkey, while in savanna or grassland there are never more than two, or at most three, and in most regions only one. Forest is admittedly a more productive habitat than savanna, but this only accounts for the greater overall biomass of primates therein, and not for the greater number of species. It could be argued that forest contains a greater variety of ecological niches than does open country, and if one overlooks for the time being the difficulty of defining a niche then this is undoubtedly true.

An open country primate has no choice but to be terrestrial, while for the forest primate an entire extra dimension is available. While some primates in forest, such as baboons or chimps, exploit both ground and trees, others, including the majority of Colobus and Cercopithecus spp, are exclusively arboreal, a mode of life that would be totally impracticable in open country. But this greater range of possible habitats is not in itself sufficient to account for the diversity of species in forest. There is in theory no reason why a small number of more adaptable species should not make full use of all the available facilities. For instance baboons are generally regarded as savanna animals, but as Rowell (1966a) points out they have sufficient tree climbing ability to be equally at home in forest, and apart from the problems of weight mentioned above could readily exploit arboreal food sources to a much greater extent than they in fact do. A limited range of adaptable species of assorted sizes would seem quite able to exploit all the available resources. The great profusion of Cercopithecus spp, most of which are basically similar in size and build, and many sympatric, is especially striking when viewed in this light.

Some clue to the origins of the diversity of forest species in Africa may be sought in the past climatic and vegetational history of the continent. We have already seen, in Chapter 1, that the present distribution of forest was attained only very recently; during the Pleistocene there were massive fluctuations in its locality and extent. Isolation of monkey populations within limited areas of forest, an essential prerequisite to speciation, would have taken place many times, and large rivers would have divided these populations even further. The present distribution of many species and sub-species can readily be understood on such a basis. Booth (1956), for example, and more recently, Moreau (1969), have pointed out the significance of features such as the Dahomey gap, the Baoule V, and the Cross River in the speciation of forest monkeys and other animals in West Africa, and Tappen (1960) has developed a similar approach to the zoogeography of African primates as a whole. Open country animals might have fewer such barriers to contend with, and are anyway more mobile.

The initial origins of the many forest species and subspecies are thus readily explicable. In several instances, though, the barriers which separated

different populations and enabled speciation to take place have subsequently disappeared, allowing the species to mingle. This raises two questions. Firstly, how, in those cases in which the species remain distinct, is hybridisation prevented, and secondly, how is competition between them restricted to a minimum?

Under the artificial conditions of captivity hybridisation is frequent, even between species that are sympatric in the wild (Gray 1954, Chiarelli 1963); hence under natural conditions isolating mechanisms must be behavioural rather than physiological. But many of the postural and facial movements and expressions are very similar throughout the genus Cercopithecus, and while there are some circumstances under which interspecific communication would be an advantage it is obviously necessary, if the species are to remain distinct, that the signals involved in behaviour such as mating should be species-specific. The explanation may lie in the great variety of pattern and colouration, particularly of the face, to be found in the genus. The overall visual impact of similar postures would presumably be very different from one species to another. It would seem, though, that reactions to these signals

cannot be purely innate but must be greatly influenced by socialisation; the hybrid in group B appeared to be at no social disadvantage despite its distinctive appearance.

This must raise further problems in areas where mixed species parties are the rule rather than the exception. For instance Frances Miller (pers.comm.) found that, in Rio Muni, Cercopithecus monkeys were from early infancy every day often within sight and sometimes within three feet of monkeys of other species. If young monkeys are almost continually in contact with species other than their own, and the development of intraspecific relations is greatly influenced by socialisation, how are such relations kept distinct from those with other species?

As regards the problem of ecological separation, comparison with birds may be instructive. Avian species are more numerous in the tropics as a whole than in temperate zones, and within the tropics forest supports a greater variety of species than does open country. Savanna and grassland habitats are often subject to a severe dry season and hence periodic food shortage, and are thus similar in many respects to temperate regions with their marked seasonality. In forest, on the other hand, the habitat is assumed to

be more stable and fluctuations in food availability less marked. It has been suggested (Klopfer and MacArthur 1960) that under these relatively constant conditions niche size is reduced; that is individual species become more highly specialised and the number of species that can be supported in a given habitat is therefore greater. A comparable degree of specialisation would be non-adaptive for a temperate or tropical open country species, since it would render it less capable of dealing with seasonal changes in the environment.

The same argument could be applied to primates. Those in open country have a wider distribution and have undergone less speciation than forest primates; such a pattern would be expected if the open country animals were more adaptable. Man is the ultimate expression of this trend. Within forest, one would expect the various species in any one area to occupy distinctive ecological niches that overlapped but little. Is this expectation borne out by the available information?

In Budongo, some degree of ecological separation can be demonstrated between all five species, though in certain cases the overlap is considerable. It is perhaps not surprising that separation can be

demonstrated between animals as different as, say, blue monkeys and baboons; indeed competition for food between these two may be no greater than between them and non-primate creatures such as frugivorous birds, fruit bats, or squirrels. Of greater significance is the relation between the two Cercopithecus spp. There is some spatial separation in both horizontal and vertical dimensions, and some separation in diet though the overlap, in terms of plant species eaten, is extensive. Since there is no shortage of sleeping sites in forest, food is the only environmental resource for which competition is likely to be significant.

In Gabon, on the other hand, Gautier and Gautier-Hion (1969) failed to find any such separation between C.nictitans, C.cephus, and C.mona in high forest regions. Mixed species parties were the rule rather than the exception and there was no marked stratification of species in the canopy. While the diet of these three species is imperfectly known, it is basically similar, and all would often be seen feeding together at the same level and on the same food. These authors suggest that either food is superabundant and hence competition minimal, or alternatively that any disadvantage arising through competition for food is

cancelled out by advantages in the detection of predators. The coming together of different species at dusk is significant in this respect. While equal protection against predators could in theory be attained by increasing group size rather than by associating with other species, it is possible that problems of communication in forest prevent the formation of integrated groups above a certain size.

There are clear cut differences, then, between the two African study areas, and while Bernstein's (1967) data for Malayan forest primates is presented in a manner that makes direct comparison difficult, it seems that the position there may be intermediate. These contrasts could be due to differences in feeding conditions between the regions. Tropical forest is generally supposed to provide a constant and abundant supply of food, but in Budongo at least this abundance is to some extent illusory as far as the monkeys are concerned. While productivity over the forest as a whole may be relatively constant, the limited areas covered by individual monkey groups' ranges are subject to considerable fluctuation (see Chapter 4). At some times food supplies are rich and concentrated, while at others they are scattered and perhaps scarce. It is significant that

mixed parties of blue monkeys and redtails were seen feeding together for long periods only when prolific trees such as Pseudospondias or Ficus spp. were fruiting, and that under these conditions stratification of species in the canopy was not marked. If such feeding conditions are typical rather than exceptional in the Gabon forests, the greater frequency of mixed parties and apparently greater overlap in diet may be partially explained. Gautier and Gautier-Hion do not present detailed information on this point, but remark that there is some seasonal variation in the amount of fruit available, and that it would be interesting to know if polyspecific associations vary with the seasons. Alternatively, or in addition, there may be differences in predation pressure between the two areas; if it is higher in Gabon this could lead to an increase in the adaptive value of such associations.

In conclusion, then, the hypothesis that forest monkeys occupy small and distinctive niches is as yet unsubstantiated. Clearly, though, niches need to be defined much more precisely than has been practicable to date. At the level of analysis required the grosser concept of niche is unsatisfactory; one can

talk in broad terms about niches for, say, leaf eaters or fruit eaters, but at a finer level niches can only be defined in terms of the precise way in which particular species exploit all aspects of their environment. Two species might be very similar in their general ecology and yet be found to overlap but little when analysis is taken to a sufficiently detailed level. Problems of interspecific relations in forest monkeys present a challenging field for further research.

RELATIONS WITH NON-PRIMATE SPECIES, AND WITH MAN.

Predators.

Probably the most important predator of the blue monkey in Budongo is the monkey eating or crowned hawk eagle, Stephanoaetus coronatus (see fig. 8.12). Monkeys are said to constitute this bird's main prey (Praed and Grant 1951, Williams 1963), though it will also take other animals if the opportunity arises. These eagles were seen several times soaring over the forest, and are probably relatively common, since, as Haddow (1952) points out, they spend much of their time flying very low over and around the crowns of the highest trees and hence escape notice.

FIG.8.12 A young crowned hawk eagle on the nest.

A pair of eagles was once seen attacking a party of blue monkeys. At least 8 monkeys were sitting or feeding in the upper canopy, spread over about 40 yards. The first eagle appeared flying low over the treetops above the monkeys. These responded with a massive outburst of volley calls, chirps and squeals. Half of them at once dropped into the lower canopy, some falling free for 60 ft. before disappearing into thick foliage, and the rest remained in the upper canopy. The eagle settled within 10 yards of two adults and sat with wings extended. They threatened it vigorously. Meanwhile a second eagle appeared, weaving in and out of the branches below the top of the canopy, and attempted to seize one of the monkeys from behind. At the last moment the monkey saw it and dropped down to the bushes below. For the next five minutes both eagles alternately sat in full view in the top canopy or tried to catch monkeys while their attention was diverted by the other member of the pair. Eventually all the monkeys dropped down into thick foliage and became widely scattered, and the eagles flew off.

On a second occasion a similar outburst of noises was heard, 200 yards off, and a pair of eagles were glimpsed flying low in among the tops of the

trees, but by the time I was able to reach the spot, 10 minutes later, no monkeys were visible and the eagles had disappeared. The short volley calls that the monkeys made during these encounters were sometimes heard, at a distance, on other days, so if they are a normal response to hunting eagles incidents such as the one witnessed must be not uncommon.

The hunting behaviour of these eagles has been discussed by Haddow (1952), on the basis of his own observations and those of C.R.S.Pitman, for many years Game Warden of Uganda. It is said that the eagle swoops down rapidly on the monkey, seizes it by the head, and then drops it, presumably to avoid the risk of being bitten. Surprise seems to play a large part in the attack, though no mention is made of hunting in pairs, and escaping into the lower canopy to be the standard means of defence on the monkeys' part.

An impressive feature of the eagles' behaviour is their ability to weave in and out of the branches below the canopy, a feat that they perform with the agility of a bird only a fraction of their size. As Haddow points out, they may as a result be able to kill monkeys well below the top of the main canopy;

on three occasions captive monkeys confined to tree platforms in connection with yellow fever research were killed by eagles, though they would, of course, be far easier prey than a wild monkey.

If the range and food requirements of a pair of eagles and the monkey population within that range were known, it would in theory be possible to work out the predation pressure on the monkeys. Unfortunately, though, little such information is available. Haddow (1952) records that a 20 mile stretch of the edge of the Semliki forest supported three pairs of eagles, so ranges must be in the order of several square miles. The monkey population density for all species combined might be perhaps 800 per sq. mile, so each pair of eagles would have several thousand monkeys in its range. It is not known how often the eagles kill, but it seems likely that they would take less than one monkey a day. Assuming, for the sake of argument, that they killed 300 in a year and that their range was 30 sq. miles and hence contained about 24,000 monkeys, then one in 80 of the monkey population would be taken during the course of the year. With no definite data to go on this figure can only be a gross approximation, but it perhaps gives some idea of the orders of magnitude involved. A mortality of one in 80 would mean that

one individual would be taken from a typical blue monkey group about once every 6 years.

An occupied eagle's nest was found in another part of the forest, but unluckily only a few days before the young bird flew. The adults were not seen to bring any food to the nest, but the young bird was observed eating some dark furred animal that could have been a blue monkey. The situation of the nest, 80 ft. up in the first fork of a large mahogany, made detailed observation difficult. A search of the ground below the tree failed to reveal any monkey skulls or other remains, but the nest was so large that bones might well have remained on its rim, and anything that was pushed out might have lodged in the dense creepers surrounding the tree rather than reaching the ground.

The crowned hawk eagle is probably the only bird of prey in Budongo of sufficient size to tackle a monkey, at least an adult. On two occasions blue monkeys were seen to drop down into the lower canopy as smaller birds of prey, possibly Ayres' hawk eagles, Hieraaetus dubius, flew past in the branches amongst them. In neither instance, though, did these eagles make any attempt to catch a monkey, and the disturbances resulting from their presence were much

less than in the case of crowned hawk eagles.

The only other potential predator of any significance is the leopard, Panthera pardus. Leopards were certainly present in the forest; though I never actually saw one I sometimes came across their tracks or heard them at night, and they may well be quite numerous. They are known to be very partial to monkeys, but it seems unlikely that they would be able to catch arboreal species in any numbers. Indeed it has been said that the only time they do readily catch tree-living monkeys is when the latter have been driven down out of the trees by eagles (Haddow 1952, quoting Pitman).

In some parts of Uganda various species of monkey are killed for their skins, for food, or to protect crops. Indeed Haddow (1952) considers man the major predator of monkeys in East Africa. The spectacular black and white cape of the colobus is especially prized by many peoples. Among others the Bakonjo of the Ruwenozori foothills hunt monkeys extensively, and while in the area I saw several blue monkey skins in their possession. No evidence of hunting was found in Budongo, though, so man can probably be discounted as a significant predator of the blue monkey in that area. It was noticeable

that colobus were very much wilder than the remaining species, so they may occasionally be taken, illegally, for their skins.

Others.

Blue monkeys were every day in close contact with a variety of other tree-living creatures such as birds and squirrels. Clear cut behavioural interactions, though, were rare. On one occasion an infant blue monkey was seen to run at a black and white casqued hornbill, Bycanistes subcylindricus (see fig. 8.13), feeding 10 ft. from it, whereupon the hornbill flew off. Twice baby or infant blue monkeys were seen to run to their mothers and cling to them when hornbills made loud and raucous noises nearby. Once a male and female blue monkey that had been sitting together got up and moved away as a great blue tourace, Corythaeola cristata, settled beside them and then flew off making alarm calls. Interactions with ground-living animals were limited to reacting to the alarm barks of bushbuck (see Chapter 5).

Many of these other animals feed on some of the same sources of food as blue monkeys. Frugiverous birds such as hornbills (Bucerotidae) and touracos (Musophagidae) were often seen feeding in Ficus, Pseudospondias, or Maesopsis trees; indeed

FIG.8.13 A pair of black and white casqued hornbills.

concentrations of fruit were often first located by listening for the clamour of hornbills. Croton fruits were much favoured by various pigeons and doves (Columbidae). Similarly various squirrels such as Protoxerus stangeri, Funisciurus europas, and Heliosciurus rufobrachium frequently visited the same food sources as monkeys. Sometimes at dusk fruit bats, probably Rousettus, Micropterus and Epomophorus spp, could be seen flying into fruiting fig trees as the monkeys ceased feeding and settled down for the night. The extent of any actual competition for food is difficult to assess, particularly since the most striking aggregations of varied types of animal are seen at times when food may possibly be superabundant (cf. Haddow 1952, p.350), but it may potentially be just as significant as that between some of the primate species.

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Chapter 9

THE ADAPTIVE SIGNIFICANCE OF SOCIAL ORGANISATION

FIG.9.1 SOCIODEMOGRAPHIC DETAILS OF SELECTED MONKEY POPULATIONS.

SPECIES	LOCALITY	HABITAT	GROUP SIZE	RANGE (sq.miles)	POPULATION DENSITY	SEX RATIO overall	SEX RATIO reprod.gps	SOCIAL STRUCTURE
Cercopithecus mitis	Budongo, Uganda	Rain forest.	14 (12 - 17) n = 6	0.03	475/sq.mile	c.1:2	1:4	One male groups and solitary males.Territorial
Cercopithecus aethiops (Struhsaker 1967abcde)	Amboseli, Kenya	Thickets in semi-arid savanna	24 (7 - 53) n = 10	0.16	225	1:2.1		Multimale groups. Territorial.
Cercopithecus aethiops (Gartlan 1966)	Lolui Island, Uganda	Forest, thicket, and grassland.	12 (6 - 21) n = 32	0.06	225	1:1.3		Multimale groups. Territorial.
Cercopithecus aethiops (Gartlan 1966)	Chobi, Uganda	Riverine bush and scrub.	18 (13 - 25) n = 3	c.0.3	57	?		Multimale groups.Tolerant, with overlapping ranges.
Miopithecus talapoin (Gautier-Hion 1966,1970)	Ntsi-Belong, Gabon	Swamp forest and secondary vegetation.	82 - 115 n = 1	c.1.5	c.60 - 80	1:2		Multimale groups, widely separated due to habitat.
Erythrocebus patas (Hall 1965)	Murchison, Uganda	Open grassland.	18 (5 - 31) n = 8	c.20	c.1	?	1:7	One male groups and solitary males or all male parties.
Theropithecus gelada (Crook 1966)	Semyen Mts, Ethiopia	Montane grassland.	Herds 74(n=17) 1♂ gps 8.5(n=30)	?	?	1:2.9	1:3.9	One male & all male groups, often combined in herds.
Papio anubis (Hall & DeVore 1965)	Nairobi, Kenya	Savanna.	41 (12 - 87) n = 9	3 - 15	10	1:2.5		Multimale troops.
Papio anubis (Rowell 1966,1969)	Ishasha, Uganda	Riverine forest & grassland.	1963..35 (30 - 45) n=3	1.5 - 2	c.20	1:1		Multimale troops.
			1968..56 (29 - 74)	?	?	1:1.4		" "
Papio cynocephalus (Hall & DeVore 1965)	Amboseli, Kenya	Semi-arid savanna.	80 (12 - 185) n = 15	?	25+	?		Multimale troops.
Papio hamadryas (Kummer 1968)	Erer-Gota, Ethiopia	Arid thornscrub.	-	?	c.4.6	1:1.4	1:1.9	One male groups & other males, in large bands.
Cercocebus albigena (Chalmers 1968a,b)	Bujuko,Mabira, Uganda	Rain forest.	17 (7 - 25) n = 7	0.05	200	1:1.7		Multimale groups.
Colobus guereza (Marler 1969)	Budongo, Uganda	Rain forest.	9 (4 - 13) n = 13	0.06	c.150	1:2.8	1:3.2	One male groups & small all male parties. Territorial.
Colobus guereza (Schenkel et al 1967)	Limuru, Kenya	Rain forest.	10 (6 - 15)	?	?	1:1		Multimale groups. Territorial.
Presbytis cristatus (Bernstein 1969)	Kuala Selangor, Malaysia	'Parkland'	31 (20 - 51)	0.08	375	?	1:12.5	One male groups. Territorial.
Presbytis entellus (Yoshita '68,Sugiyama'65a)	Dharwar, India	Dry deciduous forest.	16 (6 - 32) n = 44	0.07	260	1:3.1	1:5.3	One male groups & all male parties. Territorial.
"	Orcha, India	Moist deciduous forest.	22 (5 - 50)	1.5	7 - 16	1:6	1:6	Multimale groups.Tolerant.
"	Kaukori, India	Dry scrub and cultivated land.	54	3	7	?	1:3	Multimale gps & a few all male gps & solitary males.
Callicebus moloch (Mason 1966)	Barbascal, Colombia	Rain forest.	3 (2 - 4) n = 9	0.002	c.1100	1:1		'Family' groups.
Alouatta palliata (Chivers 1969)	Barro Colorado, Panama	Rain forest	1932 17.3 (n=23)	-	-	1:2.7		Multimale groups.
			1951 8.0 (n=30)	-	-	1:3.8		" Territorial.
			1959 18.5 (n=44)	-	-	1:2.8		"
			1967 14.7 (n=12)	-	-	1:1.8		"

small, and hence perhaps not truly representative of the populations from which they are drawn. Secondly, almost all were collected during relatively short term studies, and thus take no account of long term changes in the population; as Rowell's (1969) observations on baboons at Ishasha and the many studies of the Barro Colorado howlers (summarised in Chivers 1969) show, such changes can be substantial. Thirdly, there may be considerable variation between different populations of the same species (e.g: Presbytis entellus, Yoshiba 1968); if only one population has been studied, it may not be representative of the species as a whole.

POPULATION SIZE AND DISPERSION.

On the evidence then available, DeVore (1963) suggested that terrestrial species tended to have larger groups than arboreal ones. Likewise Crook and Gartlan (1966) pointed out that groups outside forest were typically larger than those within. These generalisations are at least in part borne out by the results of more recent studies. Thus the group sizes of blue monkeys, black mangabeys, and black and white colobus are within the limits suggested by DeVore as typical of arboreal monkeys,

and the party counts given by Struhsaker (1969) for a variety of Cercopithecus and Cercocebus spp. in Cameroon suggest that group sizes in most of these species are in the same order. Of open country species only the patas monkey has small groups, for reasons that will become clear shortly.

There are, however, some exceptions to the general trend in forest monkeys. Thus Mandrillus leucophaeus, a terrestrial forest species, sometimes forms large aggregations (Struhsaker 1969, Gartlan pers.comm.), and the group of talapoins studied by Gautier-Hion (1970) was larger than most open country troops. This particular group, though, was living to some extent as a commensal of man; groups in undisturbed habitats typically number about 40 animals, less extreme though still large in relation to other forest species.

Likewise the home ranges of forest species are usually small, less than a tenth of a square mile as against several square miles for open country monkeys. Population densities are correspondingly higher. Strictly speaking comparisons between species should be made on a basis of biomass rather than number of individuals in a given area, but even so forest monkeys clearly achieve much greater densities.

Outside forest only the vervet achieves comparable numbers, and that only in the richer habitats.

The Presbytis populations that live in the more heavily wooded habitats incline rather to the rain forest than the savanna pattern in these features, while the Kaukori langurs, with their greater group size, larger home range, and lower population density, resemble open country animals such as savanna-living baboons more closely than populations of their own species. Similarly the Ishasha baboons have smaller home ranges than exclusively savanna-living populations of the same species, and the population density is in effect substantially higher since they spent 60% of their time in riverine forest and bush though it constituted only 18% of their range (Rowell 1966a).

It seems, therefore, that as Chalmers (1968a) suggests, ' ... an arboreal habitat imposes a certain uniformity on group size, population density, and home range size on the taxonomically diverse primates living in that habitat'. Blue monkeys, black mangabeys, and black and white colobus come from widely different Old World genera, and howlers are New World monkeys, yet all are remarkably similar in these features of their organisation.

The high population density of forest monkeys is presumably explained by the greater year-round productivity of forest compared to savanna or grass-land. Group size and dispersion, as Crook (1970b) points out, will be influenced by a variety of environmental factors such as potential predation and the availability and dispersion of food and sleeping sites. Many of these factors will be the same for all forest monkeys; hence some similarity in group size and dispersion is to be expected.

There is no shortage of sleeping sites in forest; thus this will not set a lower limit to group size. In open country, on the other hand, shortage of sleeping sites may lead to the formation of large aggregations (see, for example, Kummer (1968). The only predators of forest monkeys are leopards, eagles, and occasionally man. Leopards can be escaped by crossing into another tree along thin branches, and eagles by dropping from the canopy into the lowest layers of vegetation. On the other hand open country animals have no such ready means of escape from predators, and must rely either on the fighting potential of the group as a whole (baboons) or else on rapid and silent evasive action (patas). In open country monkeys limited sleeping site availability

and potentially high predation pressure will therefore favour large troops, always provided that feeding conditions permit this. Baboon troops living in relatively rich savanna are consistently larger than typical forest monkey groups. Patas groups, on the other hand, are again small, presumably because their habitat is not sufficiently productive to support a large troop on an area that can readily be covered during a day's ranging. Potential predation pressure is still high, but the patas' slender build and great speed enable it to outrun all but the fastest predators.

Forest monkeys differ from open country ones, then, in that predation pressure and the availability of sleeping sites will set little constraint on group size. The availability and dispersion of food will therefore be a major ecological determinant. At first sight, however, it is not immediately clear why groups of the sizes characteristic of forest monkeys should arise as a direct response to feeding conditions, particularly since such conditions may vary considerably between, say, fruit eaters and leaf eaters. It can be suggested that group size is influenced only indirectly by feeding conditions, and is determined rather by intergroup relations. This hypothesis is elaborated below.

Most forest-living monkeys so far studied are territorial, while most open country ones are not. Exceptions are found in both categories, however, and detailed scrutiny reveals that territoriality is related not to forest living *per se* but to the high population density commonly attained in forest. Thus the *C.aethiops* populations at Lolui and Amboseli, which attain densities comparable to those of forest monkeys, are territorial. On the other hand vervet groups at Chobi, where the habitat is degraded and the population density lower, are tolerant of one another. Similarly langurs at Dharwar where numbers are perhaps artificially high as a result of recent forest clearance (Yoshiba 1968) are territorial, while those living at lower density in deciduous forest at Orcha are tolerant.

Territoriality is a widespread phenomenon in mammals and birds, and many functions have been ascribed to it (see, for example, Hinde 1956). A common argument is that the holding of a territory enables animals to ensure for themselves and their young an adequate food supply for all or part of the year. While direct evidence that primate territories have a comparable effect is lacking, it seems plausible to suggest that at high population densities

territoriality would be advantageous to individual group members in ensuring them and their offspring sufficient food throughout the year. In the absence of a territorial system, parts of the habitat might become overexploited at certain times, and some monkeys suffer from food shortage as a result.

There is a limit to the size of the area that can be defended if the energy expended in so doing is not to outweigh the advantage gained by its exclusive use. Interchange of loud calls commonly plays a major part in intergroup spacing in forest species (see p.183). While calling in itself involves no great expenditure of energy, calls would only be of value in keeping other monkeys away were they periodically reinforced by actual aggressive interaction. Since blue monkey volley calls are audible at well over half a mile, it would in theory be possible, if calling <u>alone</u> were effective in preventing incursions, for a male to defend a territory a mile in diameter merely by sitting in the middle and shouting. In practice territories are of such a size that any point on the perimeter can be reached in three or four minutes. As already mentioned in Chapter 5, mature males were on occasion seen to move off rapidly towards the source of calls on the edge of their territory. The

ability to detect intruders, again less easy in a large range, and to move across and expel them before they have had time to eat a significant amount, must therefore set constraints on territory size more rigid than those imposed purely by the carrying power of spacing calls.

Territory size would also presumably be affected by population density. At high densities the chances of incursion by neighbouring animals would be greater, and hence the area that could economically and effectively be defended smaller.

If territory size is thus limited, group size may be restricted by the carrying capacity of the territory. Ellefson (1968), for example, argues that gibbons are unable economically to defend an area large enough to accommodate more than six animals. This may perhaps account for the small group size of many forest species, and in extreme cases such as the gibbon for the existence of pairs rather than groups with more than one adult of either sex.

If this argument linking territoriality and group size is correct, one might expect an increase in population density from an already high level to be accompanied by a reduction not only of territory size but of group size also. Observations on the howling

monkeys of Barro Colorado (summarised in Chivers 1969), the only forest species for which long term data are available, suggest that this may indeed by the case. Thus between 1959 and 1967 the population density probably increased, while group size and the area used exclusively by a single group in a month's ranging declined.

We have already seen, in Chapter 4, that the distribution of food in tropical forest is far from even. This is especially true of fruit, and also, though perhaps to a lesser extent, of palatable leaves. The more patchy the food, the larger would be the area a group of monkeys would have to defend to ensure for themselves a sufficient supply. Similarly large animals would need more food than smaller ones, and again, other things being equal, would need a greater area to satisfy their needs. Either or both these factors might result in the area needed to support a group being so large that it would be unable to defend it against the incursions of neighbouring groups. This is in effect the situation in most open country species; since their ranges are largely two dimensional rather than three dimensional, a given area contains much less food. In forest, predation pressure and sleeping site availability set

no lower limit to group size; the difficulty can hence by overcome, up to a point, by progressive reduction in numbers. Beyond this point, though, territoriality would be impracticable, and with it would go a major constraint on the size of groups.

This may account for some of the exceptions to the general pattern of group and range size in forest primates, such as drills and chimps. Chimpanzees in Budongo depend largely on rich and scattered food sources such as Ficus, Maesopsis, Pseudospondias, Morus and Antiaris fruits (Reynolds and Reynolds 1965, Sugiyama 1968b), and must therefore range over a wide area. While the population as a whole may be divided up into 'regional populations' of perhaps 50 or so animals, these have ranges several square miles in extent and relations between adjacent regional populations are pacific. Individuals come together and split up again, forming aggregations of varying size depending on feeding conditions. The picture pieced together by Gartlan (pers.comm.) from fragmentary observations suggests that drills also range over comparatively large areas, and have considerable flexibility in their pattern of dispersion. Reliable party counts ranged from 14 to 179.

Rather different considerations apply in the case of the talapoin. Neighbouring talapoin groups seldom if ever come into contact since suitable habitats are linear and discontinuous in distribution (Gautier-Hion 1970). If a population was isolated in an area small in relation to the mobility of the animals, and food was scattered, there would be no great advantage to any individual in holding a territory. If one part of the range was over-exploited, new feeding sites could always be reached with little difficulty. Population density, and hence group size, would be adjusted to the carrying capacity of the area as a whole. Populations in larger areas, on the other hand, might be expected to be divided into small, territorial groups.

SOCIAL STRUCTURE.

When one turns from population size and dispersion to a consideration of the details of social structure of forest monkeys, the picture is not one of uniformity but of considerable and perhaps unexpected diversity. Earlier reviews (e.g: DeVore 1963, Crook and Gartlan 1966) considered forest monkeys as living either in multimale troops with roughly equal numbers of males and females (e.g: Cercocebus albigena, Alouatta palliata), or more rarely in small 'family parties' of a single pair of adults with associated young (e.g: Callicebus moloch). Blue monkeys, however, live in one male groups, and further recent work has shown that other forest monkeys do so as well (Presbytis entellus, Sugiyama 1964 , P.obscurus, P.melalophus and P.cristatus, Bernstein 1968, Colobus guereza, Marler 1969, and probably other forest Cercopithecus spp, Struhsaker 1969). Moreover there are considerable differences within these broad categories of social structure. Extragroup males in the blue monkey, for example, are solitary, while in P.entellus at Dharwar they form all male parties. Diversity of social structure among forest monkeys is thus as great as that among open country species; no particular type of structure can be said to be characteristic of one or the other environment.

This lack of close correspondence between environment and social structure may in part be due to the gross nature of the classification of habitat types. It is clearly mistaken to regard 'forest' as a uniform environment. There is no hard and fast distinction between forest on the one hand and savanna or grassland on the other; all types of intermediate are found. Those habitats that are classified as forest differ greatly in their structure, vegetational composition, and pattern of seasonality. Even within a particular type of forest there may be several different ecological niches. Thus while some aspects of the habitats of forest monkeys may be very similar, others may differ substantially.

Crook and Gartlan (1966) considered the one male group structure, then described only in hamadryas, gelada, and patas monkeys, to be an adaptation to periodic food shortage. Their argument was as follows: 'The presence of several large males, only functional in mating and playing no part in rearing young, results in the consumption of much food not used in maintaining the species. ... the one male groups of P.hamadryas, E.patas, and T.gelada are more adaptive in that less food per reproductive unit goes to individuals not involved in rearing young'. (Crook and Gartlan 1966). The advantage of the one male

group structure was thus seen as accruing to the species. No mention was made as to how such a structure might have arisen through natural selection operating on the individual, nor is this made explicit in Crook's (1970b) most recent review of the topic. The argument can, however, be couched in such a way (Crook, pers.comm.). Thus it would be to the advantage of individual males to prevent other males from feeding in close proximity to young that they had sired, and hence the mothers of those young: by so doing they would minimise the risk of their gemetic contribution to the next generation being reduced through competition for scarce food items.

Crook (1970b) accounts for the existence of one male groups in certain forest species by suggesting that they also may be living under conditions of poor food availability. In the absence of pronounced seasonal changes in feeding conditions, he argues, numbers will be closely regulated by the more or less constant level of resources. Food may be abundant, in other words, but then so are the monkeys themselves. As far as the individual animal is concerned, food may be scarce throughout the year.

This argument is perhaps an oversimplification. Over the forest as a whole productivity may be more or

less constant, but this is not true of the home ranges of individual monkeys. Most forest trees, particularly the upper canopy species, grow not in large stands but rather singly or in small clumps (see figs. 4.3 and 4.4). The range of a group of monkeys may therefore include only a few of any one tree species. For instance the ranges of groups A, B,C and D included between them only five large fig trees. Over the forest as a whole fig trees fruited continuously from September 1966 to March 1967, but the fruit on any one tree would last only for a few days. Thus in any one group's range there would be a plentiful supply for perhaps a week and none at all thereafter. As regards individual groups, therefore, the pattern would be one not of constant food availability but of brief periods of plenty with interludes of comparative shortage. (See also Chapter 4).

There are nevertheless difficulties in assuming that food is ever in really short supply. Were this so one would expect the monkeys to be forced to feed almost continually. In practice, even when food is widely scattered they are inactive for much of the day. It could be argued that quality of food rather than quantity is the critical factor. Thus an animal

that was prepared to eat old leaves would never be short of food in terms of sheer bulk, but might suffer from dietary insufficiencies and hence perhaps be less likely to breed successfully. Indeed it is a necessary consequence of the argument linking territory and group size outlined above that food <u>should</u> in some way control numbers. Our knowledge of the ecology of forest monkeys is at present so limited, though, that any such suggestions can only be speculative. Even in open country monkeys such as the gelada potential or actual competition for food has yet to be demonstrated.

In view of these difficulties, it may be of value critically to re-examine arguments for the adaptiveness of one male groups.

The mere fact that one male monopolises several females does not <u>in itself</u> reduce intraspecific competition for food. Only if there were sufficient <u>spatial</u> separation between non-reproductive males and the rest of the population for competition for food to be reduced would a one male group structure be adaptive in the manner that Crook and Gartlan (1966) suggest.

An additional advantage might accrue to individuals in reproductive groups were 'surplus' males to be driven into the poorer parts of the habitat at times of food

shortage, and hence perhaps to suffer relatively higher mortality. Demonstration of a more disparate overall sex ratio in populations having one male groups than in those with other types of social structure would hence provide support for Crook and Gartlan's thesis. The absence of any such contrast, however, would not in itself invalidate the hypothesis.

The available evidence on spatial separation is equivocal. In the gelada, herds tend to split up at times when food appears to be in short supply, with one male and all male groups foraging separately. Even when both types of group are aggregated into herds, all male groups tend to wander further from the safety of the cliffs than do one male groups, and hence to exploit slightly different parts of the habitat (Crook 1966). Likewise patas all male groups or solitary males are typically widely separated from the one male groups (Hall 1965). In hamadryas, on the other hand, there is little or no evidence for any such separation.

In the blue monkey, solitary males were seen more often on the edges of groups' ranges than within them, but sightings of such males were too few to ascertain the extent to which their ranges overlapped with those of groups. Bernstein (1968) failed to observe any

extragroup males in his population of Presbytis cristatus despite the very disparate sex ratio in one male groups, suggesting that 'surplus' males might be living elsewhere in possibly less favourable habitats. On the other hand all male groups of P. entellus at Dharwar lived in the same area as the one male groups, though the latter were generally able to drive them away if they came near (Sugiyama 1965a).

In both forest and open country, therefore, there are varying degrees of separation between one-reproductive males and the rest of the population. Whether such separation is in every case sufficient significantly to reduce intraspecific competition is debatable. Competition for food may be direct ... one animal supplanting another at a source of food, or indirect ... one animal eating food that would later be found by another had it not done so. To eliminate the latter type of competition mere temporal separation in the use of a common area might not be sufficient; non-reproductive males might have to be excluded altogether from some part of the reproductive groups' ranges. In species such as Papio hamadryas and Presbytis entellus there appears to be no such exclusion.

Turning now to consideration of overall sex ratios, the evidence is once again equivocal. As has already been mentioned above, the interpretation of sex ratios is far from straightforward. Firstly, there may be substantial variations between different groups in the same population. Ratios in P.anubis troops at Awash, for example, ranged from I:I.5 to I:3.3 (Aldrich-Blake et al, in prep.). There may be comparable variation within a single troop over a period of a few years (Rowell 1967). Ratios based on small samples may therefore be unrepresentative. Secondly, ratios are affected not only by differential mortality of the sexes but also by differences in the time taken to attain maturity (see p.100); a disparate sex ratio cannot therefore be taken as conclusive proof of differential mortality. Thirdly, and perhaps most important, extragroup males may in species such as patas and blue monkeys be harder to locate than one male groups. Supposed overall sex ratios for such species may therefore be biased in favour of females.

If the overall ratios in fig. 9.1 are considered, it will be seen that those that have been determined with any certainty range from I:I to I:6 in multimale troops, and from I:I.4 to I:3.I in populations with one male groups. There is no clear tendency for

overall ratios to be more disparate in populations having the latter type of social structure.

If the one male group structure is indeed an adaptation to periodic food shortage, it might be expected to have arisen among other groups of mammals in species subject to similar ecological pressures. The system is widespread in other mammalian orders. In some cases there is good evidence that it favours the survival of females and young at the expense of nonreproductive males. Jarman (1968), for example, found that in certain ungulate species with a one male group structure 'surplus' males were not only forced to occupy separate and inferior ranges during the dry season, but also suffered greater mortality as a result. On the other hand it is difficult to see how a one male group structure could confer such an advantage in animals such as seals. In other mammals as in primates, therefore, the evidence in favour of Crook and Gartlan's hypothesis is suggestive but not conclusive.

It is hence pertinent to ask what factors other than food shortage might cause one male groups to evolve. It can be suggested that such groups could arise through sexual selection (Orians 1969, Goss-Custard, Aldrich-Blake and Dunbar, in prep.). Natural

selection favours those individuals that make the greatest genetic contribution to succeeding generations. Since the males of most species of monkey play little part in rearing their young, a major and perhaps the only way in which a male could increase his contribution to the next generation would be by fertilising more females. There would hence be competition between males for females. Unless females differed greatly in the viability of the young that they produced, those males that were able to obtain the most exclusive access to the largest number of females would, other things being equal, leave most offspring. It seems reasonable to suggest that exclusivity of mating can more readily be attained in a one male group than in a multimale troop. Food shortage may therefore not be a necessary or even a sufficient condition for the evolution of one male groups; competition between males may be the critical factor.

Indeed it is difficult to see how food shortage <u>alone</u> could give rise to one male groups. We have already seen that some degree of spatial separation between non-reproductive males and the rest of the population is necessary for the latter to benefit from reduced competition. But how could such spatial

separation develop unless the relations between individual animals were already such that females had strong affinities with some males and only weak affinities with others? Some process such as sexual selection would seem to be essential at least in the initial stages of the formation of one male groups. That members of such groups may in certain cases attain an additional advantage through competition for food being reduced cannot be taken as identification of the critical factor responsible for their evolution.

If sexual selection is a major factor in the evolution of one male groups, one must ask why all monkeys have not developed this type of organisation. Here the various ecological factors previously suggested as influencing social structure may again be invoked. Predation pressure, for instance, would place a premium on the formation of multimale troops in open country; indeed this appears to be the only ecological factor that would actively favour the evolution of such troops. Monkeys that habitually forage far from the refuge of trees or cliffs must either be capable of outrunning predators or else have sufficient fighting ability as a group to deter attack. Since males are larger than females, the

fighting potential of a group would be increased more by the addition of males than of females. This is not to say that the greater size of males has arisen as an adaptation for group defence (cf. DeVore 1963); such dimorphism too can be explained by sexual selection (Crook and Gartlan 1966, Struhsaker 1969). It would be to the advantage of an individual male to allow other males to associate with 'his' females if the increased protection against predators his young thereby attained was greater than the disadvantage of lesser exclusivity of mating. While the additional males could attain equal protection against predators by associating in all male groups, they would not then have so great a chance of siring young. Membership of a multimale troop would therefore be advantageous to all males even if some sired many more offspring than others.

If the suggestion that protection against predators is a major factor in the evolution of multimale troops is correct, such groups might be expected to occur only in habitats where potential predation pressure is high. This expectation is only partially in accord with the available evidence. Black mangabeys and talapoins, for example, have multimale groups, yet the predators of forest monkeys ...

leopards, eagles, and man ... are not such as can be combated by group defence. Again, while many populations with multimale troops do live in areas where predators are common, others, such as the Lolui Island vervets and many macaque populations living in close association with man, do not. Recent elimination of predators from the habitat would be an adequate explanation in only a few cases.

Previous authors who have been struck by the lack of close correspondence between social structure and ecology (e.g: Chalmers 1968b, Struhsaker 1969) have emphasised the importance of phylogeny as a determinant of social organisation. Thus Struhsaker (loc.cit.) points out that ' ... each species brings a different phylogenetic heritage into a particular ecological scene'. This may in part account for some of the apparently contradictory pairings of ecology and social structure. The black mangabey, for instance, may owe its multimale group structure as much to the close relationship between Cercocebus and the baboon-macaque group, of which multimale troops are characteristic, as to present ecological conditions.

A species' phylogenetic heritage may set limits to the degree of modification of which its social structure is capable, and the rate at which any such

change can occur. Some species might thus be prevented from colonising certain habitats. Others, however, might be capable of so doing if their present social structure did not put them actively at a disadvantage. A one male group structure, for instance, might be a handicap in colonising open country, whereas a multimale structure would be no hindrance in the colonisation of forest.

While both phylogenetic heritage and proximate ecological factors may influence social structure, they should not be viewed as distinct classes of variable. Behavioural tendencies characteristic of particular taxa cannot have arisen independently of environmental selection pressures; they must, in the long term, themselves have been moulded by ecological factors. The issue, therefore, is not so much whether phylogenetic heritage or present ecological conditions play the greater part in determining social structure, but the rate at which such structure can change in response to changes in the environment. Vervets in the predator free habitat of Lolui, for example, may have multimale groups because predation was a key factor in the evolution of the social structure of the species as a whole. Relaxation of this selection pressure may have been too recent for their organisation to have changed.

The available information on social structure suggests that some taxa are more labile in their organisation than others. In some there is no flexibility even at the generic level, while in others there is mutability even within species. All members of the genus Macaca so far studied, for example, have multimale troops. Likewise with the exception of the hamadryas all populations of Papio spp that have been investigated live in multimale troops, even in arid regions with low predation pressure (Aldrich-Blake et al, in prep.). The genus Cercopithecus shows flexibility between species but not, apparently, within species. Thus the vervet populations at Lolui, Amboseli and Chobi all have multimale groups despite the contrasts in feeding conditions and predation pressure between the three areas. On the other hand colobines show lability not only between but also within species; witness the contrasts between different populations of Presbytis entellus in India and of Colobus guereza in Africa.

While our knowledge of many taxonomic groups is too scanty for generalisations to be more than tentative, the most adaptable taxa appear, paradoxically, to be those that show the least flexibility in their social structure, at least in the

limited sense that the term has been used. Baboons of the superspecies cynocephalus are found over the greater part of Africa, and in habitats ranging from rain forest through various types of savanna to arid thornscrub. Likewise macaques range from North Africa through India to the Far East, and are equally at home in the winter snows of Morocco and Northern Japan, the humid heat of the jungles of Asia, and as commensals of man in the cities and villages of India. The more intelligent and individually adaptable species thus appear to some extent to have become emancipated from some effects of the environmental pressures moulding the social organisation of other animals. This trend reaches its ultimate conclusion in man.

This should not be taken to imply that man and other higher primates are wholly immune to environmental influences, but rather that the interaction between gene pool and environment is complicated by cultures or traditions resulting from social learning. The role of what could be termed 'social selection' in the evolution of primate societies has been little stressed in the preceding discussion, but its influence must be pervasive.

CONCLUSION.

In this brief review of certain aspects of primate social organisation, some early generalisations and hypotheses have been shown to be supported by the newly available evidence on forest monkeys, some to be oversimplifications, and others to have been erroneous. Many of the ideas put forward above may likewise prove to be misplaced in the light of further research. Field studies of primate behaviour have only recently moved beyond the purely descriptive stage to a point at which major problems can be identified, hypotheses formulated, and the information to test them collected. If this study of the blue monkey helps further to reveal the extent of our ignorance, it will have served its purpose.

SUMMARY

Chapter 1. The monkeys and the forest.

The history of primate field studies is outlined, and it is pointed out that forest monkeys have been largely neglected until recently. Generalisations about primate social organisation have therefore been based on a biased sample.

The taxonomy and distribution of the Cercopithecus mitis group is described: the group contains about 20 subspecies, which are found in isolated areas from Ethiopia south to Natal and west to Angola. This discontinuous distribution is discussed in relation to the recent climatic and vegetational history of Africa.

The appearance and distribution of the blue monkey, C.mitis stuhlmanni, is described.

The ecology of the Budongo forest is outlined, and the vegetation of the study area described in detail. The luxuriance of the vegetation rendered observation difficult; this problem was in part overcome by the cutting of an extensive network of tracks.

Chapter 2. Population structure.

A discrete group structure was not readily apparent in the blue monkey; the animals were encountered rather in small parties of varying size and

composition. Some of this variation in party size is shown to be an artifact of the conditions of observation, and some to result from the behaviour of the animals themselves. Behavioural and other evidence suggests that discrete groups do exist, but that the dispersion of each group within its range varies greatly depending on feeding conditions.

The size and composition of six groups were determined. Mean group size was 14. With one exception, each group contained only one mature male. Solitary males were sometimes encountered. The home ranges of four groups were determined; average range size was 0.031 sq. miles. Adjacent ranges over-lapped marginally.

Attention is drawn to the contrast between the final picture of blue monkey population structure and the impression that would be gained by superficial observation. Short term studies of forest monkeys may be actively misleading.

Chapter 3. Daily activities and use of habitat.

Quantitative data on the daily activity cycle and use of canopy layers are presented. During the dry season feeding and movement were largely confined to the early morning and evening, but during the rains

activity was spread more evenly over the day. The monkeys were seen more often in the middle than in the lower or upper layers of the canopy, and there were seasonal differences in the use of canopy layers.

The distance travelled by an individual monkey in a day's ranging varied from 150 yards to 1000yards. Groups did not move as integrated units: examples of the splitting and coalescence of small parties are given.

The monkeys did not have regular sleeping sites, nor did the whole group come together to sleep. There was no evidence for any nocturnal activity.

Chapter 4. Diet and movements in relation to food supply.

The diet of blue monkeys consists mainly of fruit (in the wider sense of the word), young leaves and shoots, buds, and flowers, and is supplemented at times by insects and other arthropods. Most of the monkeys' food was provided by less than 30 species of tree, but several others were eaten occasionally.

Seasonal variations in feeding conditions are outlined, and the relation between the dispersion of the monkeys and that of their food supply described and discussed.

Chapter 5. Social behaviour I. (Aspects of communication)

Theoretical problems and practical difficulties in the study of communication are discussed. The various calls made by blue monkeys are described, and quantitative data on the circumstances under which each is given and the reactions of other individuals are presented. The vocal repertoire of C.mitis is compared to that of other Cercopithecus spp. The relative importance of vocal and visual signals in different types of habitat is discussed.

Chapter 6. Social behaviour II.

Expected frequencies of interaction between the various age-sex classes are calculated, and their use in statistical comparison with observed values discussed. It is pointed out that numerical data on the behaviour of forest monkeys may be subject to various sources of bias, and cannot therefore be taken at face value.

Behaviour patterns involved in social grooming are described. Quantitative data on the frequency, initiation, duration, and termination of grooming sessions are analysed in exhaustive detail. Adults other than mature males both groomed and were themselves groomed more often than expected on a random

basis. Infants groomed less but received rather more grooming than expected, largely as a result of an excess of grooming by females. Mature males did not play a prominent part in grooming, and juveniles participated in many fewer interactions than expected. The significance of grooming interactions is discussed.

'Mouthing' behaviour is described, and its frequency amongst the various classes analysed. The movement was generally directed by young animals to older ones. It may serve to identify the food another animal has been eating, and has perhaps become ritualised as a 'greeting'.

Chapter 7. Social behaviour III.

Sexual behaviour is described. Copulation was observed only rarely. Putative dates of birth of 13 babies are given: there is no distinct birth season, but some suggestion of a concentration of births during the two dry seasons.

Maternal behaviour and infant development are described. The young of C.mitis appear to develop rather more slowly than those of C.aethiops. Blue monkeys differ from many other species in that other members of the group take little interest in females with babies; indeed the latter may be involved in

fewer interactions than other females. The young animal has little social contact with monkeys other than the mother for the first 2½ months. Infants may play together from 2½ to 3 months of age onwards, but other classes are seldom involved in play. Play is less elaborate than in other species.

Agonistic behaviour patterns are described. Such behaviour was very rare: only 29 instances of threat or aggression between members of the same group were observed, and in only one of these was any animal bitten. More subtle manifestations of tension between individuals ... 'social monitoring', or interactions having an approach-retreat pattern ... were likewise infrequent. There was no clear cut spatial arrangement within the group, and no one class tended to lead or to initiate movements.

The frequencies with which the various classes sat together are analysed. Babies, adults other than mature males, and to a lesser extent infants sat with other monkeys more than expected, and mature males and juveniles less.

Intergroup relations are discussed. Agonistic encounters, characterised by the giving of loud calls and 'bouncing' displays by mature males, and by threats and chases between other monkeys, were observed on 14

occasions. Most such encounters were clearly related to rich food sources in the overlap zone between adjacent groups' ranges. At other times members of different groups appeared to avoid one another. Loud calls given by the mature males may help to keep groups apart.

The relevance of salient aspects of blue monkey behaviour to concepts such as dominance and social roles is discussed.

Chapter 8. Relations with other species.

Mixed parties of blue monkeys and Cercopithecus ascanius or Colobus guereza were commonly encountered, but appeared to be temporary aggregations rather than coordinated social units. None of these species showed any tendency to associate with baboons or chimps, both of which are known to have carnivorous propensities. Quantitative data on the relative frequency with which the various species were seen in association with blue monkeys are analysed, and behavioural interactions between species are described.

There are varying degrees of ecological separation between the different primates in the forest. While no species confined itself exclusively to any one layer of the canopy, quantitative evidence shows that colobus tended to occupy higher and redtails lower

levels than blue monkeys. Baboons and chimps were based on the ground, but might ascend into the trees to feed. The relative frequency of species varied in different parts of the forest: baboons were based on the forest edge and foraged out into the savanna and a short way into the forest, redtails were found in young colonising forest and along the edge of tracks and clearings, and the remaining species were found deeper into the forest. There are differing degrees of overlap in diet as assessed by species composition and part of the plant eaten, blue monkeys and redtails overlapping substantially with one another and with chimps, but less with colobus and baboons.

These findings are contrasted with comparable data from West Africa and Malaya (Gautier and Gautier-Hion 1969, Bernstein 1967), and their theoretical significance is discussed.

The hunting behaviour of the crowned hawk eagle, probably the major predator of the blue monkey, is described, and the proportion of the population that these birds might kill estimated. Relations with other non-primate species are described.

Chapter 9. The adaptive significance of social organisation.

Early generalisations and hypotheses regarding primate social behaviour are re-examined in the light

of newly available evidence on the blue monkey and other forest species. The group sizes and home range areas of most forest monkeys are similar, and tend to be smaller than those of open country monkeys. Most forest species so far studied are territorial, while most open country ones are not. Ecological factors affecting group size and range are discussed. It is suggested that territory size is related to a group's ability economically and effectively to defend a given area against intruders, and that group size is in turn determined by the available resources within that area.

Diversity of social structure among forest monkeys is found to be as great as that among open country species: in particular, the blue monkey and other forest species have the one male group structure formerly considered an adaptation to seasonally arid environments (Crook and Gartlan 1966). Arguments for the adaptiveness of this type of structure are critically scrutinised. It is suggested that food shortage alone is not a sufficient and perhaps not a necessary condition for the development of one male groups. Attention is drawn to the possible role of sexual selection in their evolution.

The significance of phylogenetic heritage and of social learning and culture as determinants of primate social organisation are alluded to.

It is pointed out that we still know very little about many aspects of primate behaviour.

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